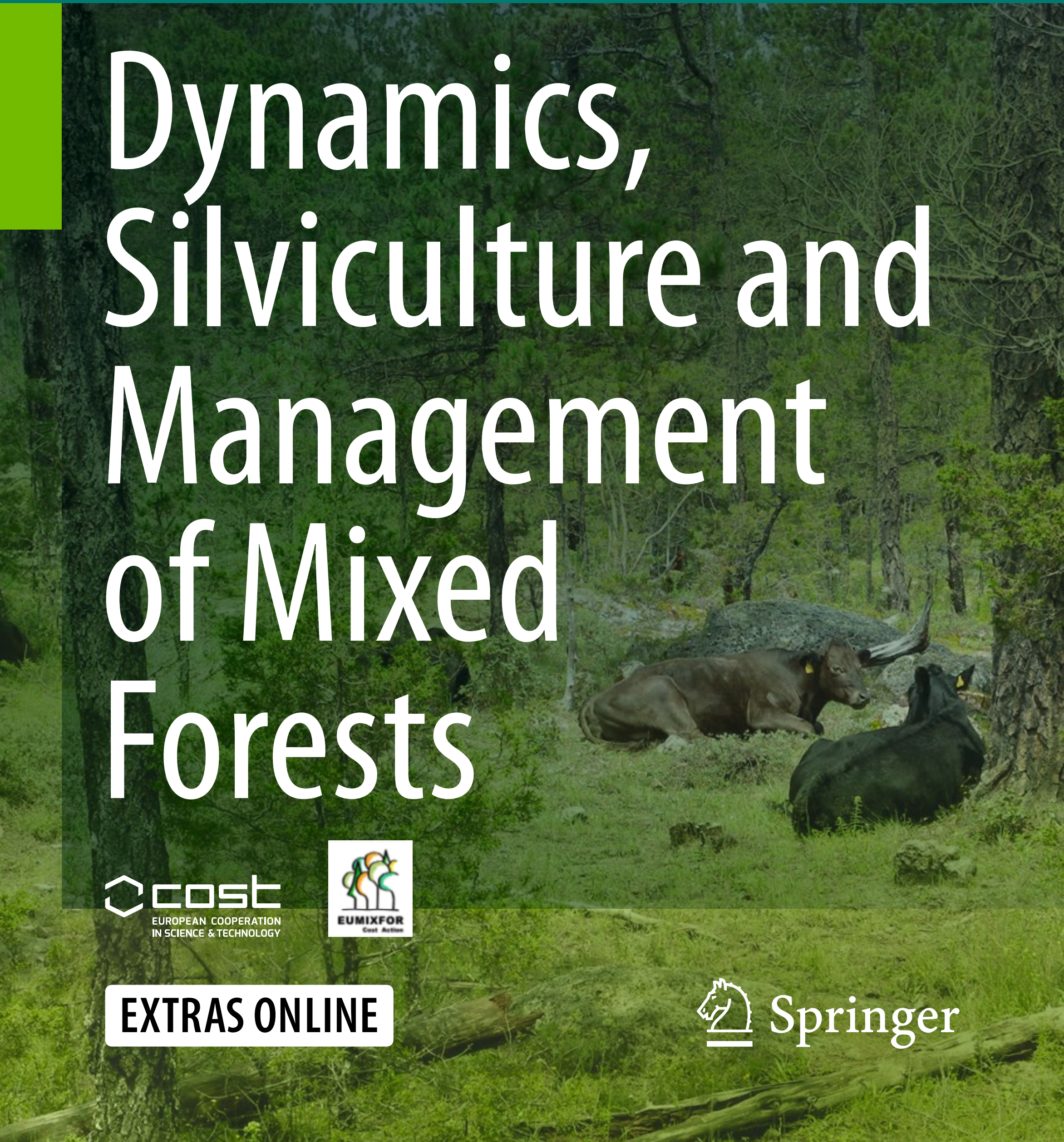
Managing Forest Ecosystems

Andrés Bravo-Oviedo · Hans Pretzsch
Miren del Río *Editors*



Dynamics, Silviculture and Management of Mixed Forests

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Managing Forest Ecosystems

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Aims & Scope

Well-managed forests and woodlands are a renewable resource, producing essential raw material with minimum waste and energy use. Rich in habitat and species diversity, forests may contribute to increased ecosystem stability. They can absorb the effects of unwanted deposition and other disturbances and protect neighbouring ecosystems by maintaining stable nutrient and energy cycles and by preventing soil degradation and erosion. They provide much-needed recreation and their continued existence contributes to stabilizing rural communities.

Forests are managed for timber production and species, habitat and process conservation. A subtle shift from multiple-use management to ecosystems management is being observed and the new ecological perspective of multi-functional forest management is based on the principles of ecosystem diversity, stability and elasticity, and the dynamic equilibrium of primary and secondary production.

Making full use of new technology is one of the challenges facing forest management today. Resource information must be obtained with a limited budget. This requires better timing of resource assessment activities and improved use of multiple data sources. Sound ecosystems management, like any other management activity, relies on effective forecasting and operational control.

The aim of the book series Managing Forest Ecosystems is to present state-of-the-art research results relating to the practice of forest management. Contributions are solicited from prominent authors. Each reference book, monograph or proceedings volume will be focused to deal with a specific context. Typical issues of the series are: resource assessment techniques, evaluating sustainability for even-aged and uneven-aged forests, multi-objective management, predicting forest development, optimizing forest management, biodiversity management and monitoring, risk assessment and economic analysis.

More information about this series at http://www.springer.com/series/6247

Andrés Bravo-Oviedo • Hans Pretzsch
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Editors

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Foreword

Despite the fact that forests with two or more species represent 70% of the forested area of Europe, widespread interest in mixed species management and the existence of national policies that encourage it, management of mixed species stands has been limited by a lack of experience with mixed stands. This has resulted from historical focus on management for single-species even-age stands. COST Action FP1206 – EuMIXFOR provided an outstanding opportunity to bring together researchers and managers to examine and explore options for managing mixed species forests and has supported information exchange and development of several valuable references, including this synthesis.

The potential values of mixed species stands in terms of contribution to biodiversity, ecological services, resilience, and sustainable forest management are emphasized throughout the book. The dynamic nature of mixed stands and the influences of static and dynamic management practices are also discussed.

Definitions (Chap. 1), methods for characterizing mixed stands (Chap. 2), and data sources currently available for examining mixed stands with description of promising new research approaches (Chap. 3) are presented. Chapter 4 discusses factors influencing natural regeneration of mixed species stands and identifies knowledge gaps. Results indicate that thinnings may be useful in enhancing seed production and development of regeneration, that managing groupwise may be more effective than managing stemwise, and that deer pose a serious challenge for regeneration of palatable species.

The influence of composition and other stand characteristics on growth, structure, and wood quality are explored in Chap. 5. European mixed species stands produce up to 30% more stem volume than monocultures, largely due to mixed stands supporting higher densities and crown projection area. Chapter 5 provides a number of recommendations for research to answer fundamental questions, support development of growth models, and support development of practical guidelines for managing mixed stands.

Survey results compiled by the EuMIXFOR project (Chap. 6) indicate that: (a) timber production remains the dominant focus in many areas managed as mixtures, with protection of soil and water being more important in some cases; (b) that use of the uniform shelterwood regeneration method is widespread; and (c) that game pressure is a widespread issue in the management of mixed species stands across most of Europe. Case studies from four countries illustrate different aspects of mixed species silviculture (Chap. 7). These case studies suggest that: (a) successful development of mixtures relies on establishment of desired species either during stand initiation or understory reinitiation stages; (b) management of mixtures generally results in some movement away from shade intolerant to more shade tolerant species; (c) mixtures take time to develop and may require tending to ensure development toward desired targets; (d) deer browsing can limit success; (e) Forest Development Types provide a useful framework that integrates information about tree species that are adapted to particular sites and influences of management and composition on stand dynamics; and (f) development of practical and feasible approaches to mixed species management requires focus on a limited number of major species, at least initially.

Chapter 8 describes the main temperate mixed forest types of Chile and Argentina and discusses ecological issues and management strategies. It is interesting to note that 50% of the 13.6 million ha of Chilean forests are mixed, while only 5% of the 3.29 million hectares of Argentina's temperate forest are mixed.

Establishment and management of mixed species plantations is reviewed in Chap. 9, with emphasis on their value in increasing resilience, reducing risk and uncertainty, and providing a broader range of ecosystem services and non-timber products than monocultures.

Models that can represent stand dynamics and growth of component species are important to our understanding of potential outcomes and to development and testing of suitable management practices. As indicated in Chap. 10, modeling mixed species stands is complicated since interspecific (as well as intraspecific) interactions; the effects of climate, site, browsing, species identity, and other factors; and the interactions between factors need to be considered.

Chapter 11 explores the economic aspects of mixed forest management and discusses valuation of ecosystem services and application of constraints analysis, joint production analysis, and portfolio approaches. Results from four case studies indicate that mixtures may often be superior to monocultures in terms of yield, timber economic value, and joint production of ecological services.

The concluding chapter provides a summary and discusses how enhancing and promoting mixtures of tree species can serve to meet a broad range of goals provided that we understand the "interplay between environmental drivers, site- and species response" and we account for "multiple social demands from forests." The need for long-term experimental research including sampling along gradients of environmental conditions, stages of stand development, and species mixtures to better capture the dynamics of growth and yield in mixed forests is emphasized. Growth models, stand simulators, and scenario assessments are identified as key elements needed for designing mixed species stands and evaluating results. The authors suggest that silvicultural prescriptions developed from research or arising from previous experience need to be quantified, simplified for transfer to managers, and demonstrated in the field.

The large team of coauthors brings together a broad scope of expertise relating to a wide range of forest types, environments, and management challenges. This book discusses issues, includes practical recommendations, and identifies current research needs. It provides an outstanding resource for anyone interested in mixed species management and research.

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March 15, 2018

Phil Comeau

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Chapter 1
The Role of Mixed Forests in a Changing Social-Ecological World

Andrés Bravo-Oviedo

Abstract There is a growing attention to mixed forests in the world. Their capacity to cope with mitigation and adaptation to climate change by increasing resilience and lowering risks is pinpointed as an opportunity to highlight the role of tree species-rich forests as part of complex socio-ecological systems. However, analyses of the performance of mixed forests are hampered so far by the lack of a reference definition of mixed forest and the multiple species- and site-specific cases that lead to incomplete knowledge in the delivery of ecosystem services as compared with pure stands. Here, a proposal of definition of mixed forests is discussed along with the performance of mixed forests in the context of the delivery of selected ecosystem services. It is stressed that the analysis of the interaction between structure and functioning and the constraints imposed by changing bio-geophysical conditions is a key issue to fulfill the increasing demand of ecosystem services and the challenge of policy decisions that might affect forest systems (e.g., the transition to bio-economy). Opportunities for forest managers and researchers are highlighted accordingly.

1.1 Mixed Forests: Setting the Scene

Near one third of the earth land area is covered by forests. Natural forests occupy 93% of the global forest area with a declining annual rate of 1.3 million hectares between 2010 and 2015, while planted forests represent 7% of land with an average annual growth between 1990 and 2015 of 3.1 million hectares (FAO 2015). Forest

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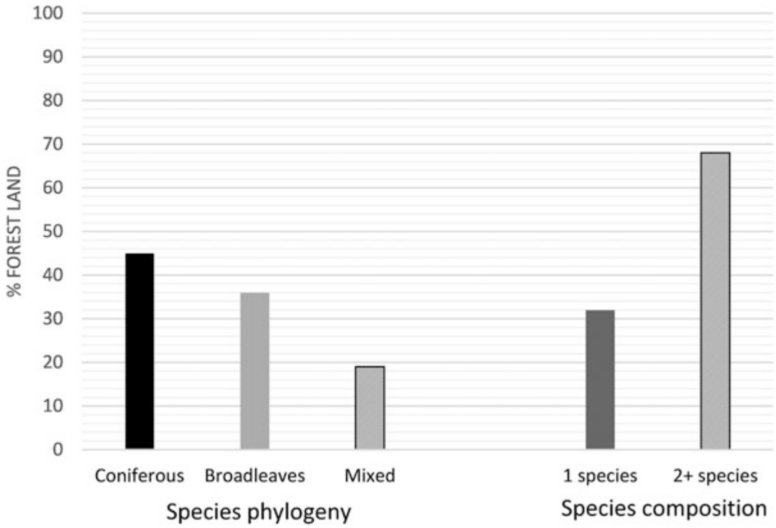

Fig. 1.1 Forest land sharing of mixed-species stands in Europe using different classification methods. Mixed forests using a species phylogeny approach occupy 19% of forest land, whereas using a compositional approach the sharing increases up to 68%. (Data from Forest Europe 2011)

functions result in ecosystem services required by human societies like, among others, timber, water quality, nutrient cycling, or biodiversity preservation. Managing this huge natural capital in a sustainable way is a worldwide challenge.

Sustainability of forest management aims, among other features, the maintenance of biodiversity and the potential to fulfill relevant ecological, economic, and social functions (EU Commission 2013). Improving, expanding, and managing mixed forests can contribute to this goal as long as they are more resilient and resistant (Jactel et al. 2009, 2017), more productive (Kelty 1992; Paquette and Messier 2011; Pretzsch et al. 2015), or more structurally diverse (Pretzsch et al. 2016a) than single-species forests. In addition, the steady decrease of single-species forests in some parts of the world urges the need to include mixed stand management options in the forest policy agenda.

However, at the global scale, it is difficult to compare the performance of mixed forests if the same forest composition and structure is considered either mixed or pure depending on forest regulations and the definition used. For example, in early reports about the state of Europe's forests mixed forest is constrained to broadleaved and coniferous mixture (Forest Europe 2011). This classification of mixed forests gives 19% of total forest land in Europe as mixed (Forest Europe 2011), whereas if it is considered the number of component species, irrespective of their phylogenetic group, the sharing increases up to 68% (Fig. 1.1).

Classification of mixed forests according to phylogenetic groups is based on the scientific evidence that mixing effects are better achieved by species with complementary use of resources (Forrester 2014a; Forrester and Pretzsch 2015) associated with differences in height growth pattern, phenology, or crown and root structure (Kelty 1992). This topic has built a large body of research about mixing effects in mixtures of broadleaves and conifers (del Río et al. 2016, 2018; Pretzsch et al. 2015 and references therein) although mixing effects are also found in species within the same phylogenetic group (Pretzsch et al. 2013b; Riofrío et al. 2017).

Attempts to define mixed forests have been based on three related features: species composition, structural features, and those based on forest development phases (Bravo-Oviedo et al. 2014). The starting point for a mixed forest is the trivial fact that there must be at least two tree species. However, this definition is usually accompanied by a threshold beyond which the stand is considered pure. Toumey and Korstian (1947) defined pure stands as those where number of trees is 80% or more of the overstory is of a single species. However, if less than 10% in the overstory is of a commercially or silviculturally valuable species, the stand is classified as mixed. This adds to the commercial value of the species a preeminent role irrespectively if the species actually does or does not play a significant role so to affect the development of the other species or the functioning of the ecosystem. The weakness of the compositional approach is that a two-species stand with a proportion of 80:20 can be considered pure if one species is not commercially valuable, whereas another stand with two commercial species in the same proportion might be considered mixed.

Calculation of the threshold or species proportion is also of concern when it comes to compare the performance of mixed versus pure stands. Two species can have different growing space requirements, and the area potentially available for each species might be also different leading to different outcomes (Dirnberger and Sterba 2014; Rio and Sterba 2009; del Rio et al. 2018). The structure of the mixture can also have a great impact when characterizing and defining mixed forests. Leikola (1999) proposed a three-axes classification system for mixed forests that takes into account the horizontal arrangement of trees (stem-, row-, or groupwise), the type of vertical stratification (single-, multistoried), and the number of species present in the stand. However, the composition and structural approaches are static, whereas mixed stands are part of a developmental dynamic affected by disturbance regime and environmental gradients that conferred the mixture a role of transition (Spies 1997).

Bravo-Oviedo et al. (2014) analyzed previous attempts to define mixed forests and proposed a reference definition encompassing the following aspects: composition, structure, development phase, and function. A mixed forest stand was defined as *a forest unit, excluding linear formations, where at least two tree species coexist at any developmental stage, sharing common resources (light, water, and/or soil nutrients). The presence of each of the component species is normally quantified as a proportion of the number of stems or of basal area, although volume, biomass, or canopy cover as well as proportions by occupied stand area may be used for specific objectives. A variety of structures and patterns of mixtures can occur, and the interactions between the component species and their relative proportions may change over time.*

This definition was considered a reference to make comparisons between mixtures in order to make generalizations of performance of mixed forests in the delivery of ecosystem services. This is similar to mixed versus pure stands studies where site conditions must be similar for the species under study, i.e., the triplet approach (Heym et al. 2017; Ruiz-Peinado et al. 2018). In case two mixtures are compared, the reference definition for both should indicate that they are in a similar developmental stage, that the same methods to calculate the proportion threshold are used, and that the vertical and horizontal structure and the main interaction driving the stand dynamics are considered.

1.2 The Quest for Sustainability

1.2.1 Mixed Forests and Biodiversity Goals

Mixed forests dynamics and mixed planted forests must be included in the accountability of forest resources as they might contribute to the achievement of United Nations Global Forest Goals and associated targets as well as the Aichi biodiversity targets in a more straightforward way than single-species forests and plantations (Table 1.1).

1.2.2 Viewpoints of Sustainable Forest Management

Natural resource management is usually considered a tool to prevent overexploitation of resources and biodiversity loss (Bravo 2014). The way this management is performed can follow a gradient of complexity from the anthropogenic perspective of dominant use (managing one single resource) to the ecocentric precept of the ecoregional paradigm (managing ecological processes) shifting the scale from the management unit to the landscape ecosystem unit (Yaffee 1999).

Sustainable forest management (SFM) is the global forest sector response to the need for sustainable development while maintaining biodiversity and forest ecosystems services provided in response to the demand for forest resources of society (EEA 2015). However, the concept of SFM is not the same for all stakeholders (FAO 2015), for example, Davis et al. (2001) presented four viewpoints of sustainable forests based, among others, on the relationship of human to forests and the outcomes generated. The first viewpoint is *sustained yield* where humans dominate nature and the main product is timber; *multiple use-sustained yield* in which humans control nature but other values than timber are also recognized, i.e., water purification, recreation, and wildlife; the third viewpoint is *naturally functioning forest ecosystems*, here humans are excluded, and only natural structures, processes, and species in its native range are considered valuable. Finally, in the *sustainable human-forest ecosystems* viewpoint, humans and nature coexist, and all forest outcomes either commodities or natural processes are considered.

All the previous viewpoints and paradigms have been historically identified and so does the management and silvicultural alternatives associated with them.

Table 1.1 Examples of the role of mixed forests on the achievement of Global Forest Goals (GFG) and associated Aichi biodiversity goals (ABG)

Global forests goals	Aichi biodiversity goals	Potential contribution from mixed forests
1. Reverse the loss of forest cover worldwide through SFM, including protection, restoration, afforestation, and reforestation, and increase efforts to prevent forest degradation, and contribute to the global effort of addressing climate change	A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society	Mixed-species forests have a great potential as benchmark for studies focused on biodiversity loss effects
	B: Reduce the direct pressures on biodiversity and promote sustainable use	Increasing the abundance of tree species in stands by planting new mixtures or adding species would improve the resilience capacity of forests contributing to safeguard ecosystem integrity
	C: Improve the status of biodiversity by safeguarding ecosystems, species, and genetic diversity	
2. Enhance forest-based economic, social, and environmental benefits, including by improving the livelihoods of forest-dependent people	A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society	Mixed forests are more attractive to public because of a larger portfolio of ecosystem services needed by society which, in turn, would be more prone to participate in decision-making processes
	D: Enhance the benefits to all from biodiversity and ecosystem services	
	E: Enhance implementation through participatory planning, knowledge management, and capacity building	
3. Increase significantly the area of protected forests worldwide and other areas of sustainably managed forests, as well as the proportion of forest products from sustainably managed forests	B: Reduce the direct pressures on biodiversity and promote sustainable use	Planted forests have an important role to buffer pressure over species-rich natural forests. If the plantation is planned as mixed species, it would also improve the resilience and the portfolio of ecosystem services enhancing the benefits for human well-being
	C: Improve the status of biodiversity by safeguarding ecosystems, species, and genetic diversity	
	D: Enhance the benefits to all from biodiversity and ecosystem services	
4. Mobilize significantly increased, new and additional financial resources from all sources for the implementation of SFM and strengthen scientific and technical cooperation and partnerships	E: Enhance implementation through participatory planning, knowledge management, and capacity building	The increasing importance of mixed and complex forests has gained attention of funding schemes like COST Actions (www.mixedforests.eu) and ERA-Net projects (www.reform-mixing.eu) which are examples of scientific and technical cooperation and capacity building through specific tools oriented to early career investigators

(continued)

Table 1.1 (continued)

Global forests goals	Aichi biodiversity goals	Potential contribution from mixed forests
5. Promote governance frameworks to implement SFM, including through the UN Forest Instrument, and enhance the contribution of forests to the 2030 Agenda	A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society	Biodiversity loss and public concern due to unprecedented catastrophic events, like large wildfires, can be buffered by more resilient forest structures like those found in mixed forests

GFG 6 is not included as it is not associated with ABG in the original formulation

Kimmins (2004) considers the following phases – unregulated exploitation, perception of scarcity, exploitation of remote forests, simple regulations, administrative norms, and conservation and management practices, whereas Gamborg and Larsen (2003) identified five management phases including exploitation, traditional methods, sustained yield, multiple use, and "back-to-nature," whereas Pretzsch (2007) refined Yaffee's (1999) classification of natural resource management from a historical European perspective of forest management where the multiple use preceded the dominant use due to scarcity of timber and fuelwood in the seventeenth century. More recently, Duncker et al. (2012) have proposed a classification of forest management according to 12 decision elements independent from historical processes, resulting in five management approaches based on the intensity of human intervention: passive management (no intervention), low-intensity management (close-to-nature silviculture), medium intensity (combined objective forestry), high intensity (even-aged forestry), and short rotation forestry (plantations).

Depending on cultural and developmental stages, all viewpoints of sustainable forests and management paradigms, whatever the classification, can be found in the world. In certain areas they can be found within the same geographic area, like in Europe where about 95% of forest area is under management (EEA 2016) and contrasting management alternatives are being discussed within the same region. In this debate the traditional management of forest resources based on the regulation of age or size distribution in time and space has been put into question, and new silvicultural alternatives have arisen to emulate the natural disturbance regime (Ecological Forestry, Kohm and Franklin 1997), to follow natural regeneration processes (Close-to-Nature, Bauhus et al. 2013; Brang et al. 2014) or to maintain closed canopies (Continuous cover forestry, Mason et al. 2003; Pukkala and von Gadow 2012).

Mixed forests are usually considered part of management systems aiming to mimic natural structures associated with low-disturbance regime or with little human intervention ranging from single-tree selection to group systems (Pach et al. 2018). They can be also seen as part of dynamics or final state, depending on the development forest type (Mason et al. 2018).

New alternatives to traditional forest management are rooted in the idea that forests are complex biological systems (Nocentini 2011) following Levin (1998) who presented ecosystems as complex adaptive systems (CAS). Although CAS is not a new concept, it has been incorporated into forestry literature recently (Puettmann et al. 2008; Messier et al. 2015). The main properties of forests as a complex adaptive system are heterogeneity, hierarchy, self-regulation, openness, adaptation, memory, nonlinearity, and uncertainty (Filotas et al. 2014), all of them needed to adapt to changing conditions (Messier et al. 2015). In the line of the CAS approach, forests interact with social and economic systems (Ciancio and Nocentini 2011) being part of a complex social-ecological system (SES sensu Ostrom 2009, 2007) where attributes like resilience, adaptation, and transformation, along with governance mechanisms, must drive the decision-making (Walker et al. 2004).

The performance of mixed forest as integrated part of a complex and adaptive socio-ecological system is both a research and policy issue as multi-species forest has been proposed as an alternative to single-species forest in a global change context. Such comparison needs a clear definition and characterization of mixed forests to disentangle the mechanisms driving mixed forest stand dynamics.

Forestry requires the characterization of the target species, site conditions, and the current and desired forest structure in order to accomplish management objectives. Adoption and implementation of the best management alternative within a portfolio of well-established management regimes is straightforward if such alternative has been already tested in analogous forest stands, where analogous means similar site conditions, species composition, and forest structure. However, in the case of mixed forests, the adoption of management alternatives is hampered even by slight differences in species composition or forest structure (del Rio et al. 2018). For example, the growth efficiency of Scots pine, measured as the volume increment divided by the species proportion by area, increases with increasing proportion of beech modulated by stocking degree (Condés et al. 2013). A solution might be the adaptation of known silvicultural practices to site-specific conditions and designing new alternatives which would include specific experimental designs and changing proportions (Kelty and Cameron 1995; Puettmann et al. 2008).

1.3 The Social-Ecological Context

A social-ecological system (SES) is defined as a linked system of humans and nature where humans are part of nature (Berkes et al. 1998), which is in accordance with Davis et al.'s (2001) *sustainable human-forest ecosystem* point of view and can be traced back to Dietrich (1953 *in* Assmann 1971) who pointed the need to deal with the relationships between human society and forest community.

In a SES framework, both the ecological and social components are affected by bio-geophysical conditions and political and economic decisions (Redman et al. 2004) that would alter the ecosystem response and the societal demands of services from forests (Fig. 1.1). For example, increasing catastrophic events like wild fires

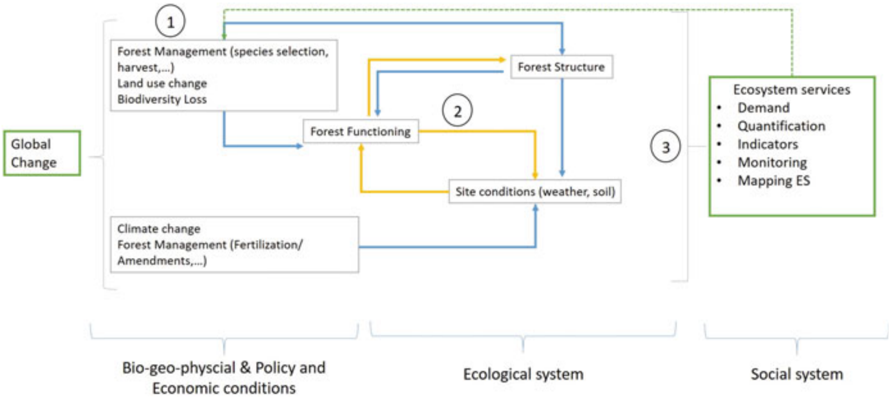

Fig. 1.2 Integrated framework of relationships between drivers of change and components of forests as social-ecological systems. The framework is valid for single- and multi-species forests. In mixed forests, the feedback loop between forest ecosystem structure and functioning is critical, and it is highly dependent on the interspecific interactions (niche complementarity, facilitation) and the species-specific effect on site conditions (presence of a nitrogen fixing or nutrient-rich species). (After Redman et al. (2004), Pretzsch (2014), and Pretzsch et al. (2015))

exacerbated by longer periods of drought can condition political decisions regarding forest management practices (point 1 in Fig. 1.2) which would affect forest structure and forest functioning via the inner feedback loop between both of them (point 2 in Fig. 1.2). The outcomes generated by changes in forest policies and management must meet societal demands of ecosystem services (point 3 in Fig. 1.2). In this example, the society might demand a rapid recovery of forests orienting policymakers to promote a more resilient forest composition and structure (dashed line in Fig. 1.2). However, it might be the case that society would require the same provision of ecosystem services prior to disturbance and decisions would be focus on creating resistance. The assessment of performance of mixed forests requires specific analysis of intra- and interspecific relationships in the feedback loop between structure and functioning. The performance can be assessed in terms of changes in structure and functioning (Pretzsch et al. 2016a).

While approximately 80% of global forest area is in public ownership (FAO 2015, 2016), more than half of forest area in the EU27 countries is owned by private individuals (Pulla et al. 2013). Hence, in the European context, the private forests are of key importance in improving SFM. Compared to public ownership, the smaller scale of management operations and the wide set of ecosystem services utilized support stand and tree diversity in private forests and provide opportunities for mixed stand management.

1.4 The Quest for Multifunctionality

The concept of ecosystem function is ambiguous meaning different things for different people (Jax 2005). Frequently, ecosystem function has been treated as synonymous of ecosystem process following (Wallace 2007). Here, a forest function is an ecosystem property resulting from the action of one or several ecosystem processes, whereas an ecosystem service is a benefit for humans generated by natural processes and functions at the ecosystem level, which may be subject to monetary or nonmonetary valuation (Maes et al. 2016).

Long-term biogeochemical processes contribute to the delivery of services like nutrient regulation, water purification, erosion control, or production of biomass and raw materials. However, human needs have a finer time, and space scale and services from forests must be collected in the short run. Forest management is the response to the need of ecosystem services in a relatively short time and spatial scale. The achievement of an ecosystem service is at the expense of the achievement of others leading to simplification of functioning and structure in many managed forests.

Forests are home of multiple life forms originating high values of biodiversity. Managing such biodiversity with the aim to satisfy human needs and, at the same time, preserve it is challenging. The interplay of human settlements and forests has been described as a circular path from unmanaged natural forests to exploitation first and from sustained and sustainable management to back-to-nature management more recently (Gamborg and Larsen 2003) parallel to the natural resource management from dominant use to ecoregional management (Yaffee 1999).

However, maximization of revenues first and optimization in the latter does not necessary mean multifunctionality and simultaneous delivery of multiple ecosystem services. One of the reasons is the impossibility to maximize all needs in a forest compartment or forest management unit. The idea anchored in timber-oriented forestry is that by managing forest for timber production (dominant use), all other functions and associated services follow. However, this motto has been recently questioned (Puettmann et al. 2008), and it has opened the debate on how to reach multifunctionality.

Biodiversity and species richness have been pointed as determinants to increase (multi)functionality in diverse terrestrial ecosystems (Hector and Bagchi 2007; Vilà et al. 2013; Gamfeldt et al. 2013). For a single function, e.g., biomass production, tree richness loss of 10% would result in volume PAI loss of up to 66% at a global scale (Liang et al. 2016). However, diversity-productivity studies are hampered if confounding factors, like successional stage, climate, disturbance regime, or management, are not accounted for (Vilà et al. 2005) urging the need to include biotic and abiotic factors as multifunctionality drivers (Maestre et al. 2016).

The challenge of multifunctional forestry is to identify trigger points where the decreasing of one function is not compensated anymore by the increase in another factor (Gamfeldt et al. 2008); in other words, there is a need to understand the mechanisms and quantify the trade-offs between functions when forest managers face a multipurpose objective, like increase timber yield without decreasing tree species richness.

Forest management has seen biodiversity as a conservation issue (Mori et al. 2017) where iconic species or monumental trees are preserved if they are found in production forests. However, the role of forest biodiversity as a driver of multifunctionality and ecosystem services might play a significant role in the future of forestry to meet societal demands where the importance of mixed forests is substantially increasing. The challenge of managing multifunctional mixed-species forests is to deal with multiple functional trade-offs and the subsequent ecosystem services trade-offs.

A complex and multiple function situation, such as mixed forests, requires specific research. Van der Plas et al. (2016) coined the term *jack-of-all-trades* when multiple functions are provided at intermediate levels in species-rich forests based on the idea that species identity has an important role as different species provide different services (Hector and Bagchi 2007). However, the way multifunctionality is measured is based on additivity of functions which could mask complex interactions acting at different levels. One limitation in biodiversity-(multi)functionality studies is the difficulty to account for system properties that emerge when upscaling from research plots or stands to ecosystem level, i.e., emergent properties in complex systems. Improved metrics of multifunctionality are needed to make correct assessment of mixed forest performance.

1.5 Novel Mixed Forests

The reduction in global forest cover is partially offset by an increase in the area of planted forests. However, the loss of biodiversity due to deforestation is rarely compensated. Recently, the role of plantations has been claimed to constitute an opportunity for natural restoration after disturbance including degrading effects due to human activity during the Anthropocene (Paquette and Messier 2010). When properly designed plantations can support the conservation of native biodiversity (Brockerhoff et al. 2008) and buffer the increasing pressure over natural forests while ameliorating soil conditions in degraded lands (Tesfaye et al. 2016). However, monoculture plantations are usually seen as green deserts because of its lack of tree species richness and associated simplification of functions due to intensive management for timber. This is also a simplified point of view as many plantations in the world are designed to control erosion or to mimic initial successional stages by planting pioneer species. The importance of plantations in our changing world will increase, and forest managers and policymakers should consider new management alternatives to get advantage of species resilience capacity. Lindenmayer et al. (2015) suggest treating plantations as novel ecosystems in a socio-ecological context by integrating them in a functional zoning approach (Messier et al. 2009) which would result in increasing diversity at the landscape level. At the forest or stand level, a plantation can be designed to be more resilient and resistant by increasing the functional diversity and species richness from the design phase by planting new species in an existing monoculture (Paquette and Messier 2013; Urgoiti and Paquette 2018). However, if increased species richness means increased forest resistance, it is not a straightforward relationship (Grossiord et al. 2014).

There also exists a decoupling among stakeholders' perceptions about mixed plantations. Whereas forest managers are reluctant to plant mixtures due to an apparent loss of production (Carnol et al. 2014), visitors and local communities often prefer more diverse structures than monocultures (Nielsen et al. 2007). However, managed forests with intermediate densities are preferred to unmanaged dense forest or more intense managed ones (Jensen and Skovsgaard 2009). Reconciling users' needs with practitioners and owners' rights requires scientific evidence that proves the cases where there is a positive biodiversity-ecosystem (multi)functioning relationship. Initiatives such as TREEDivNet can help in disentangling the benefits and drawbacks of mixed plantations (Verheyen et al. 2016).

1.6 Mixed Forests Performance and the Delivery of Selected Ecosystem Services

Mixed forests are a clear example of complex adaptive systems embedded in a social-ecological framework where ecosystem services synergies and trade-offs are exacerbated compared to monocultures. Multiple demands from forests are better accomplished by mixed forests providing than a single commodity is not preferred or that the associated loss of direct benefit is compensated by increasing resilience and resistance to disturbances.

With this premise in mind, EuMIXFOR COST Action is a global network of researchers and managers that has significantly contributed to this research with the aim of establishing a long-lasting European research network on mixed forests, which can contribute to the increase of knowledge, the sustainability of management, and the future expansion, conservation, and improvement of mixed forests on the basis of science, innovation, and rural development in Europe. Under these premises EuMIXFOR has focused on the exchange and increase of knowledge about the performance of mixed versus pure stands in the delivery of ecosystem services.

Human well-being is highly linked to the continued supply of ecosystem services (Hassan et al. 2005), and biodiversity is a key regulator of such supply (Diaz et al. 2005). The increasing attention to mixtures has built a large body of research about the performance of mixed forests versus pure stands with the double aim of assessing the amount and direction in the delivery of ecosystem services and the mechanisms explaining the observed patterns. Literature is highly biased toward the following ecosystem services.

1.6.1 Provisioning Ecosystem Services

1.6.1.1 Fibers and Other Materials

There is increasing evidence that mixed forests produce more timber than pure stands of the component species (Rio and Sterba 2009; Pretzsch et al. 2013a, 2015; Bielak et al. 2014). Biomass productivity also increases with species richness (Liang et al. 2016). However, lower productivity of mixed stands has been also described (Chen and Klinka 2003). Productivity of mixed versus pure stands increases with precipitation and age (Thurm and Pretzsch 2016) and might decrease with site productivity (Toïgo et al. 2015). In general, results are context-dependent, both species- and site-specific (Chen et al. 2003).

Several mechanisms have been proposed to be responsible of the observed overyielding of mixed forests (Jactel et al. 2018): complementarity or niche differentiation, facilitation or improved environment of the growing conditions of one species caused by other species, and the sampling effect or greater probability of having a high productive species when species richness increases (Thompson et al. 2014). Disentangling which mechanisms dominate is not straightforward. Ecological approaches have dealt with additive partitioning between complementarity and selection effects (Loreau and Hector 2001; Kunert et al. 2012), whereas complementarity and facilitation are usually confounded when both mechanisms lead to commensalism interactions (Larocque et al. 2013). In addition, complementarity is spatial and temporal variable (Forrester 2014b), and it might be affected by increasing stand density of mixed forests (Condés et al. 2013).

1.6.1.2 Groundwater

Forest ecosystems are central in the water cycle as they contribute to cool and increase the relative humidity by evapotranspiration; they promote rainfall, enhance both soil infiltration capacity, and recharge groundwater reservoirs (Sprenger et al. 2013; Ellison et al. 2017). They also increase water quality by hosting microorganisms responsible of water purification and filtering (Thompson et al. 2014). At the same time forests are water consumers and might affect negatively water production. There exists a correlation between forest production and water consumption where tree density and composition are key drivers. The current paradigm that predicts that increasing stand density reduces water production has been recently questioned as many studies are biased toward comparisons of young high-productive plantations against natural situations and during the whole annual recharge period instead of taking into account the whole age range and critical periods for water recharge (Ellison et al. 2017). The paradigm has been modulated at intermediate stand densities, where water recharge capacity is higher (Ilstedt et al. 2016).

Forests with high species richness have higher evapotranspiration rates (Kunert et al. 2012), but as for production, water uptake is highly species-specific

(Schwendenmann et al. 2015). Pure beech and Scots pine stands have higher groundwater recharge than their mixture, and young stands have lower groundwater recharge than mature stands (Natkhin et al. 2012). Mixed forest canopy increases the rainfall interception due to stratification and higher roughness increasing the water consumption. Groundwater is increased if the sharing of oak is high relative to Scots pine due to lower evapotranspiration rate of oak. Old stands showed decreasing transpiration which increased the groundwater recharge at higher levels than young managed stands that have higher percolation rates (Fürstenau et al. 2007), although under climate change scenarios the increasing evaporation demand from trees would decrease the percolation rate (Lasch et al. 2005).

In addition, higher productivity and density would also decrease the groundwater recharge at the stand level. In general it needs more evidence about the type of mixture (species richness and identity) and stand density to avoid irreversible water-timber production trade-offs.

1.6.2 Regulating and Maintenance

1.6.2.1 Decomposition and Fixing Processes

Litter decomposition is a key process in carbon turnover and nutrient recycling in forest ecosystems and might represent near one third of total carbon release in mixed and pure stands (Berger et al. 2010) and mixing can increase soil quality (Hu et al. 2006). As for growth and yield studies, decomposition rates in mixtures can be inferred for those found in pure stands if the mixing effect is additive. However, it might be the case that there exists some interaction between different litter types inducing nonlinearity which can produce synergistic or antagonistic effects. The "home field advantage" (HFA) hypothesis postulates that litter decomposes faster underneath the cover of the species that has generated it (Gholz et al. 2000) because of selective pressure over the decomposer community (Ayres et al. 2009); in other words, soil biota is specialized in decomposing local litter. This might have profound consequences in regulating services when management is oriented to introduce new species or when species distribution range shifts northward, because of global warming, migrating to places where soil biota is not efficient in decomposing material from new species.

Evidence of HFA has been found in boreal forests (Sanborn and Brockley 2009; Chomel et al. 2015), but rejections for HFA have been found in temperate oak-beech forests (Jonard et al. 2008), in subtropical forests (Wang et al. 2009), and in Mediterranean climate type (Sheffer et al. 2015). Discrepancies in findings might be caused by failure in setting the right questions (Prescott 2005) or by lacking control over confounding factors. For example, litter-type interactions can change over time (Aponte et al. 2012) and being affected by extreme climatic events and species richness (Santonja et al. 2015). Management can also interfered decomposition by either accelerating or slowing down the process. In those sites where low

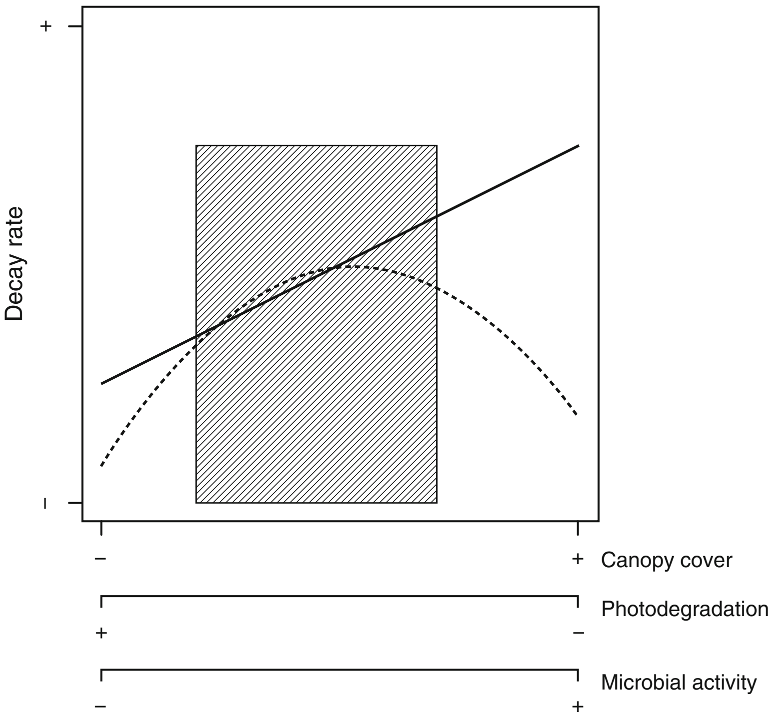

Fig. 1.3 Hypothetical litter relationship in a Mediterranean-type environment. The response is species-specific, whereas the interaction between pure and mixed stands might change based on changes in canopy cover (natural or silvicultural disturbances) and the relative importance of photodegradation and microbial activity. Bold and dashed lines represent two possible decomposition paths for two species with contrasting litter type. The gray area is the "unknown" response of litter decomposition in mixed forest which would be affected by species proportion

temperature is hampering decomposition, a reduction of stand density by thinning would increase the incident solar radiation on soils stimulating decomposition (Thibodeau et al. 2000), whereas in Mediterranean environments, where moisture conditions are limiting, the reduction of tree cover would induce soil desiccation and reduction in the decomposition rate (Bravo-Oviedo et al. 2017). Warmer conditions due to climate change might also increase the relative contribution of abiotic factors, such as photodegradation (Almagro et al. 2015, 2016), increasing the carbon release from litter to the atmosphere without recycling through the soil (Austin and Vivanco 2006).

A thorough study on the effects of tree diversity in decomposition should include comparisons with pure stands while controlling for biotic and abiotic factors mainly temperature, humidity, litter type, decomposer community, the contribution of photodegradation, management, and their potential interactions (Fig. 1.3).

1.6.2.2 Soil Condition (Carbon and Nitrogen Concentration and Stocks)

Species- and site-specific differences in productivity and decomposition rates would lead to differences in carbon storage between pure and mixed stands. Two-species boreal forests stored intermediate carbon values between component species (Cavard et al. 2010). The same has been found for mixtures of European beech, Douglas fir, and Norway spruce (Cremer et al. 2016). However, when accounting for stand stocking in temperate forests, the higher the number of species in the mixture, the higher the aboveground carbon storage (Woodall et al. 2011).

With regard to soil, there is contrasting evidence. In general, topsoil carbon and nitrogen stock is reduced in mixed stands of oak and Scots pine (Matos et al. 2010), whereas mixed forest stands can store more carbon in soils than pure stands although examples like the natural hardwoods and red pine plantations in the USA did not show differences in soil carbon (Gahagan et al. 2015).

1.6.2.3 Flood Protection

River and flash floods risk and the fraction of human population exposed to flooding events are expected to increase because of increasing heavy precipitation events (IPCC 2014). This will increase the economic impact of a natural hazard that it is already considered one of the highest in Europe (European Environment Agency 2015).

Forests mitigate the damaging effects from floods because of its water-retention capacity and runoff control. In general, the most forested the catchment, the more water retained by forest. Conifers retain more water than broadleaves, and mixed forests are placed in between although some regional and seasonal variability exists, for example, runoff is lower in mixed stands during winter in the Mediterranean bioregion, whereas broadleaved forests retain more water in summer (EEA-European Environment Agency 2015). Complementarity of water use in mixed forests might explain the higher water retention in mixed forests, but more research is needed before making generalizations as spatial variation and temporal shift in water retention exist.

Species identity should also take into account to make a throughout assessment of the role of mixture to prevent flood damage. There is a species-specific factor for water use efficiency, and this can even change if individuals are growing in mixtures (Jonard et al. 2011). Species richness has a positive effect on plant damage after flooding in grassland communities (Wright et al. 2017), but there is a lack of research about the effect of species richness or diversity in flooding disturbance or peak flows (Alila et al. 2009).

The effect of flood over species coexistence has been documented (Duncan 1993). Tree cover has been pointed as an estimate of flood control, and this research might be extrapolated to mixtures where the canopy cover can be higher because of vertical partitioning. However, repeated flooding and water logging might affect species composition as some species are sensitive to these stress factors, for example, *Fagus sylvatica* (Gessler et al. 2007).

1.7 Challenges and Opportunities for Mixed Forest Research and Management

Mixed forests are a clear example of complex adaptive systems from which forest managers and researchers can learn and test alternatives to face the current challenges that forest sector is facing, like:

1. *Increasing demand of diverse forest services*. Forest are seen as providers of multiple ecosystem services that are not usually correlated, and trade-offs emerge increasing the uncertainty and difficulty of management. For example, positive and negative trade-offs occur between species richness and ecosystem functions that lead to provisioning services (Balvanera et al. 2014). Although the conceptual framework for many studies to assess the relationship between species richness and function is the biodiversity-ecosystem functioning (BEF) approach (Scherer-Lorenzen 2014), it needed an integrated approach which incorporates the biodiversity-ecosystem services (BES) approach (Cardinale et al. 2012) including the effect of management on that relationship. Many studies, including those developed in EuMIXFOR, have found that there is strong evidence of a better performance of mixed forest over pure stands in productivity due to complementarity effects or increased relative importance of facilitation (Forrester et al. 2004; Kelty 2006; Pretzsch 2018). Mixing effects can also positively affect structural diversity of beech-Scots pine mixtures (Pretzsch et al. 2016b), whereas increasing structural heterogeneity in pure plantations might be detrimental to growth (Soares et al. 2016; Zeller et al. 2018). It is thus imperative to identify those circumstances where increasing diversity (species composition, structure, and interactions) leads to positive, negative, or neutral effects on ecosystem services.
2. *Global change* is a threat that current and future generations of forest managers must face. The idea of keeping structure and composition stable during long periods of time could lead to "failing silvicultural systems" because of maladaptation and higher susceptibility to changes (Millar et al. 2007). The ideal normal forest is being displaced by adaptive management where unexpected outcomes are not considered failures but opportunities to learn and improve the resilience of forest ecosystem. The adaptive management is not free of pitfalls (Rist et al. 2016), but approaches such as the complex adaptive systems may serve as a conceptual framework to recognize that forest systems are open, heterogeneous, hierarchical, and self-regulated whose main characteristic is the emergence of properties across scales (Messier et al. 2013). Although this framework can be easily implemented in novel ecosystems such as mixed plantations (Lindenmayer et al. 2015; Paquette and Messier 2010; Urgoiti and Paquette 2018), more

research is needed to develop feasible management options in order to broadly adopt complex adaptive systems and associated new silvicultural options (Filotas et al. 2014; Messier et al. 2015; Puettmann et al. 2015; Nocentini et al. 2017).

3. *Transition to bio-economy*. Many countries and regions are currently promoting a strategy for a resource-use efficiency and sustainable economy based on natural resources, the so-called bio-economy strategy (European Commission 2013). This new framework for sustainable growth aims to sustainably use biological resources, while ensuring biodiversity. In this new context, forestry faces a major challenge as the single resource-oriented management (i.e., timber management) is expected to move to a diverse resource-oriented management (i.e., commodities and amenities). Therefore, there is a need to assess the sustainability of complex silvicultural alternatives and theoretical frameworks in the context of bio-economy as it is estimated an increase in forest biomass use between 17% and 44% in 2020 (Scarlat et al. 2015) which means increasing use of wood and wood-related products in the energy system. However, there is not a consensus about the relationship between bio-economy and biodiversity. Marchetti et al. (2014) pointed that an increase in species richness would increase the opportunities for the bio-economy as the pool of available species and resources is higher, whereas from the other side land-use changes and decreasing biodiversity would be expected if few number of species were enough to meet the bio-economy goals (Hall et al. 2012). The potential conflict between bio-economy and biodiversity must be anticipated and mediated by rigorous research about the role of species richness in the provision of multiple ecosystem services and the subsequent trade-offs.

As in the learning-by-doing approach of adaptive management, every challenge is an opportunity in itself, and for forest managers and researchers, the following lines of activity are identified:

1. *Implementation of adaptive forest management to increase resilience*. Proactive management to deal with global change should include building resistance using well-known techniques like thinning, promote resilience using assisted regeneration, and make possible the response to change (assisted migration, new mixtures, selection of adapted provenances). The bottleneck to this opportunity is the lack of a clear integration between the effects of forest management on functioning due to changes in structure and the processes associated with those functions.
2. *Multifunctional mixed-species plantations to increase ecosystem services portfolio*. Planted forests represent 7% of forest land in the world (FAO 2015), but it is estimated to supply 50% of timber by 2040 (Kanninen 2010). The increasing importance of mixed-species plantations is supported by the increasing evidence of better performance than monocultures in terms of pest and pathogen resistance, stability to windthrow events, or higher productivity (Urgoiti and Paquette 2018). The identification of species combinations and proportions used in plantations that best meet management objectives and the mechanisms leading to best performance (complementarity, sampling effect, or insurance hypothesis (Yachi

and Loreau 1999)) deserves more attention in research programs to help make decisions on forest land management.

3. *Quantitative characterization of mechanisms behind ES trade-offs*. Forest management is objective-oriented, and because optimization of the main goal could impair the performance of another ES, it is mandatory to determine the trigger point at which detrimental effects of management jeopardize the system stability. Mixed forests provide a larger portfolio of ecosystem services, and they might be considered as a benchmark to assess the performance of ecosystem services. The inclusion of risk analysis associated with biotic and abiotic factors (pest, drought events, wildfire) and economic valuation that includes users' preferences would close the circle society-economy-ecology in mixed forests as social-ecological systems.

1.8 Concluding Remarks

Resilience thinking and adaptive management of current forest systems are needed to cope with uncertainties associated with global change. The rate of species extinction, economic and political shifts, and societal demands requires a holistic approach of forest management embedded in the social-ecological framework where forests are viewed as complex adaptive systems. Resilient forest management implies increasing options for adaptation. Among alternatives increasing the number of tree species is pointed as a priority in many regions of the world urging the need for understanding of mixed forests dynamics. Although interest for complex structures has existed from the very beginning of forestry as a scientific discipline, the shift toward more diverse, complex, and resilient forest structures is more straightforward than ever.

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Chapter 2
Characterization of Mixed Forests

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Abstract An appropriate, common interpretation of stand structure characteristics is a key element to better understand forest ecosystem ecology and dynamics. Standards for characterizing the structure, dynamics and productivity of even-aged pure stands are well developed, but such harmonized concepts and methods for mixed forest stands are lacking. Here we compile a comprehensive set of measures, indices and methods at stand level to characterize and evaluate mixed stands. The chapter is organized according to the main components of the structure of forest

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stands; hence it includes (1) the most relevant concepts and approaches to describe stand density as a key component of stand structure; (2) stand species composition indicators and the most common species diversity indices used in the science of forest growth and yield; (3) how to describe tree distribution patterns, including horizontal spatial pattern, species intermingling and vertical spatial pattern, as well as species-specific height growth and canopy space partitioning; (4) ways to characterize tree-size distribution and growth partitioning among trees of different sizes;

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and (5) site productivity indices and methods for the comparison of productivity in mixed vs. monospecific stands. Finally we discuss some of the methodological and application challenges related to the reviewed indices and methods which require further attention.

2.1 Introduction

The current promotion of mixed stands in forest management is unquestionably due to the importance of species diversity in providing forest functions and services, as well as to their important role in forest adaptation and mitigation of climate change. Hence, there is a greater demand for knowledge regarding mixed forest dynamics and management practices, which has led to an increasing number of studies focusing on the effect of species composition on forest dynamics, growth and yield (Pretzsch 2018), as well as on silviculture on these forests (Pach et al. 2018).

Stand structure is a key element in forest dynamics and productivity (Pretzsch 2018). In even-aged pure forests, stand structure and forest dynamics can be described by few stand variables. But in more complex forest systems, a more detailed characterization of structure is needed to adequately study forest dynamics and forest productivity, as well as to develop management guidelines. Similarly, the stand development of a “normal” forest is, in general, well understood in the case of even-aged monospecific forests but not in the case of mixed forests. This makes it difficult to use and interpret, or even to define, some common variables such as stand density or productivity indices.

Decades of research in pure stands have yielded standards for characterizing their structure (e.g. Kraft’s social classes, Reineke’s stand density index (1933)), dynamics (e.g. self-thinning) and productivity (e.g. growth-density curves), as well as providing an indication of their performance through simple phytometric methods (e.g. site index). This standardization of terminology (Helms 1998), symbols (van Soest et al. 1965), establishment of experiments (Skovsgaard et al. 2006) and measurement (Prodan 1968), along with the evaluation and reporting of results (Johann 1993), is important in order to achieve comprehensive evaluation, comparison and communication in the science of forest growth and yield. The great variability in mixed forest structure, together with the lack of harmonized concepts and methods related to growth and yield in mixed stands, leads to a number of difficulties when comparing and generalizing results from research studies (Forrester and Pretzsch 2015).

In this chapter we revise and update the review about concepts and methods for characterizing the structure, dynamics and productivity of mixed-species stands done under the framework of the COST Action EuMIXFOR (del Río et al. 2016). The aim of this chapter is to respond to the need for a complete, comprehensive set of measures, indicators and methods for the evaluation of mixed stands. We describe and discuss the main methods and indices for characterizing stand density, species composition and diversity, tree spatial distribution patterns, tree-size distribution and productivity, focusing on both total stand and species levels.

2.2 Stand Density

In general ecology, density refers to the abundance of an organism within a defined area. In plant ecology, density is often defined specifically as the number of individuals per unit area (Bonham 2013). In forestry, the term is used more broadly and incorporates not only the number of trees but their size and other characteristics, to describe the degree of utilization of site resources and crowding (Dean and Baldwin 1996). Ideally, a density measure – in pure or mixed stands – should help describe and predict tree demography within a stand, including the onset and progress of self-thinning (e.g. del Río et al. 2001); susceptibility to biotic and abiotic stressors, such as pathogens and wind (e.g. Anhold and Jenkins 1987; Castedo-Dorado et al. 2009); and the size and development of tree crowns, which have consequences for tree growth (e.g. Valentine et al. 2012), stem volume and biomass allometry (e.g. Mäkelä and Valentine 2006), as well as timber quality (e.g. Hein et al. 2007).

Several absolute measures of density have been used in pure stands and can also be used in mixed stands without modification; however, their interpretation becomes more challenging. Number of organisms per unit area does not lend itself to ecological or silvicultural interpretation, when those organisms may vary in size and metabolic activity over orders of magnitude; thus, its use remains confined largely to stands in the regeneration phase in both pure and mixed stands. Basal area per hectare is easy to measure. However, its interpretation varies with tree size, even in pure stands. In mixed stands, where individual trees of the same diameter but of different species may differ in key traits such as height, crown dimensions, tolerance to shade and other stressors, or growth rate, its interpretation becomes even more challenging. As Barrett and Carlson (1990) write, “Clearly, the assumption that a tree is a tree regardless of species provides an unreasonable estimate of crowding.” Stem volume and biomass are measures of direct interest for forest management, and the allocation of biomass within a stand has important consequences for carbon assimilation (Evans 1972). However, allocation of biomass in forest trees has a historical dimension, because of the accumulation of heartwood in the stem and the response of the crown to competition. When allometric relationships are used to estimate tree volume or biomass from tree diameter or height in mixed stands, those relationships must reflect the influences of past mixture on tree growth and form. Naïve application of allometries developed in pure stands to the same species growing in mixtures may give biased or misleading results. These complexities do not rule out the utility of simple absolute measures for general descriptive purposes. However, their use for ecological and silvicultural inference is limited, since reference conditions (such as densities at which crown closure, self-thinning or other relevant stand behaviours occur) will depend on site conditions, stand development stages and the nature of the mixture being considered.

In even-aged monocultures, leaf area index (the area of foliage per unit ground area) has been hypothesized to approach a constant as a developing stand reaches closure. The reallocation of a constant amount of foliage among a declining number of stems, as those stems increase in size, is one mechanism believed to underlie observed size-density relationships (Long and Smith 1984). For example, as trees supporting a constant quantity of foliage grow taller, they also become slender relative to their height, and the resulting mechanical instability of the stems gives rise to a constraint that approximates both Reineke's (1933) relationship and the $-3/2$ self-thinning phenomenon (Dean and Baldwin 1996). O'Hara et al. (2001) developed a leaf area allocation approach to describe stocking in mixed stands of Norway spruce and Scots pine. They used published relationships between sapwood area and leaf area for these species, but noted that for portability to different sites or stand structures, new relationships might have to be developed. In principle, leaf area of stands can be measured by indirect techniques, including litterfall, hemispherical photography, analysis of transmitted light through the canopy and remote sensing; each of these is associated with assumptions and challenges for operational use (e.g. Jonckheere et al. 2004; Zheng and Moskal 2009). Leaf area of individual trees is most often assessed using allometric relationships with diameter at breast height, with sapwood area or with crown dimensions; however, such relationships are notoriously unstable between sites and stand conditions. Recent advances, such as the advent of terrestrial laser scanning, have made non-destructive measurement of leaf area somewhat more accessible, especially for research (e.g. Hosoi and Omasa 2009; Huang and Pretzsch 2010). However, scanners remain relatively expensive, and results can be sensitive to the scanner used (Ducey et al. 2013). Rapid, reliable techniques that can give consistent estimates of leaf area in extensive, operational use remain some years away.

Most approaches to characterizing density in mixed-species stands depend on dendrometric approaches, in which simple measurements such as tree diameter and height stand used as a proxy for more complex morphological and physiological variables. In many mixtures, data are available to characterize maximum density for the component species when they occur as monocultures. For example, such data might come from normal yield tables or from the long-term development of unthinned stands on permanent plots. In such cases, there are two ways to compute a density for the species mixture assuming that species-specific maximum densities are the same as in monocultures. The first is to calculate an adjusted maximum for an absolute density measure, based on the maxima of the original species and their proportions in the observed stand. The second is to compute the relative density contribution of each component species separately and then combine them. Done correctly, one might hope these two approaches would be algebraically equivalent; however, this is not always the case in practice. An example of the first approach is presented by Barrett and Carlson (1990). They note that for a mixture, with actual basal area G_i and maximum basal area $G_{i,max}$ for each species i at its observed mean diameter, a combined maximum basal area can be calculated as

$$\mathrm{G}_{\text{combined, max}} = \Sigma\, p_i G_{i,\,\max} \tag{2.1}$$

where the species proportions are defined in terms of basal area, i.e.,

$$p_i = G_i/\left(\Sigma\, G_j\right) \tag{2.2}$$

and the sums are over all species in the stand. The density (D) of the stand might then be assessed by the fraction

$$D = (\Sigma\, G_i)/G_{\text{combined, max}} \tag{2.3}$$

Examples of the second approach include the relative density (S) as computed from the partial relative basal areas of pure stands (del Río and Sterba 2009; Condés et al. 2013)

$$S = \Sigma\, G_i/G_{i,\,\max} \tag{2.4}$$

or the relative density index (RDI) as computed from the partial relative densities computed from number of trees per hectare (e.g. Hein and Dhôte 2006; Waskiewicz et al. 2013)

$$\mathrm{RDI} = \Sigma\, N_i/N_{i,\,\max} \tag{2.5}$$

Now, suppose that we evaluate stand density using the equation for D, but note that $G = \Sigma\ G_i$ is just the total stand basal area, and substitute the full definitions of $G_{\text{combined,max}}$ and p_i:

$$D = G/[\Sigma\ (G_i/G)\ G_{i,\,\max}] = G^2/(\Sigma\ G_i\ G_{i,\,\max}) \tag{2.6}$$

which clearly does not equal S except in trivial cases. The formulation of S is to be preferred, because it preserves the area contribution of the individual species (Prodan 1959; Sterba et al. 2014). Sterba et al. (2014) describe a procedure for calculating the proportions in a two-species mixture that would maintain consistency between D and S. Note that if the same formulation is used to compute $G_{i,\max}$ and $N_{i,\max}$, and the stand is sufficiently even-aged that one can treat all of the trees of a given species as having the same diameter, $S = \mathrm{RDI}$. However, equations for $G_{i,\max}$ often depend on stand height (Sterba 1987), while those for $N_{i,\max}$ often depend on stand diameter, so incompatibilities may arise in practice.

In even-aged monocultures, a wide variety of relationships combining tree size and tree number have been used to characterize stand density, including Hart's (1928) relative spacing based on tree height, Reineke's (1933) stand density index (SDI) and relationships based on the −3/2 self-thinning phenomenon (Yoda et al. 1963). Of these, Reineke's has been the most common starting point for developing mixed-species density measures. Reineke's relationship describes a self-thinning trajectory forming a straight line between the logarithm of quadratic mean diameter and the logarithm of number of trees per hectare. The self-thinning trajectory is also called the maximum size-density relationship, or MSDR. The slope of that relationship (which becomes an exponent after reversing the log transformation) was approximately -1.6 in Reineke's original (1933) study. That same slope has proven to be approximately correct in many subsequent studies, although there is also strong evidence for interspecific variation (e.g. Pretzsch and Biber 2005; Charru et al. 2012), or even intraspecific variation when the range of the site conditions is large enough (Condés et al. 2017). Such variation reflects a species' self-tolerance in a monoculture (Zeide 1985); more generally, it reflects changes in the allometry of tree form and resource use with changes in tree size, which could potentially be altered by growth in a mixed-species stand. In any case, inter- and intraspecific variations in the self-thinning trajectory may have a strong impact when using this relationship to estimate RDI in mixed stands (Fig. 2.1).

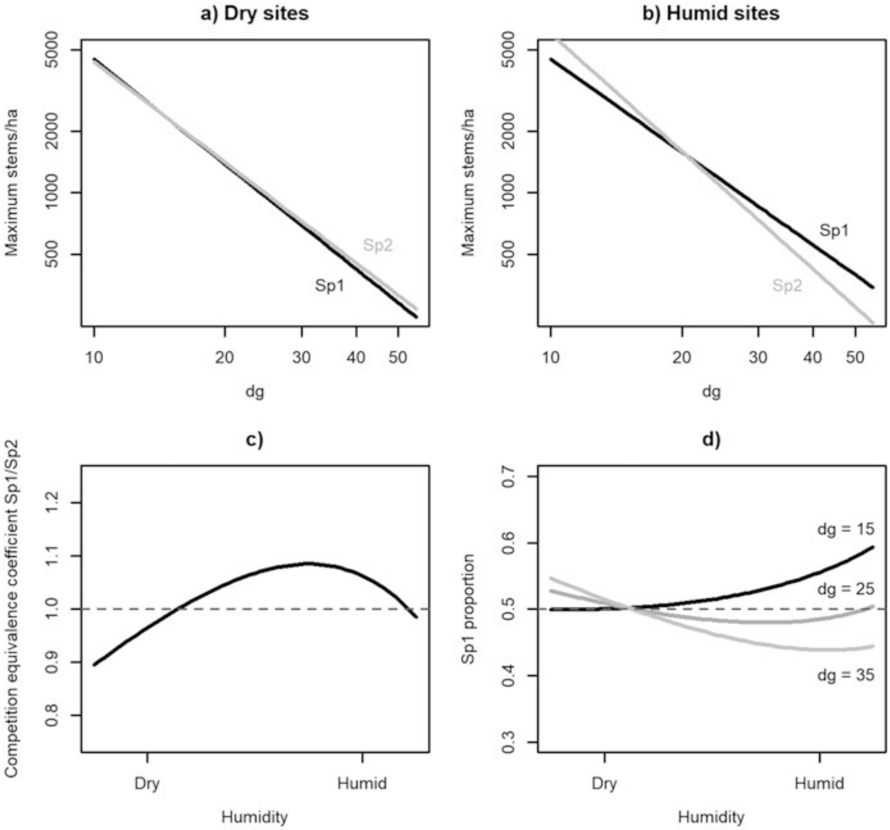


Fig. 2.1 Self-thinning lines for species 1 and 2 for (**a**) dry site and (**b**) wet site; (**c**) variation with humidity of the competition equivalence coefficient between the two species; and (**d**) variation with humidity of proportion of species 1 for different mean tree size, assuming that the two species have the same mean tree size. (Adapted from Condés et al. 2017)

However, interactions between species might cause different types of modifications of the MSDR or self-thinning trajectories (Pretzsch et al. 2012b; Pretzsch and Biber 2016). The two parameters of the line can vary for the different species and for the total stand. The intercept can be higher (or lower) meaning that the neighbourhood's interspecific interactions enable a higher (or lower) level of packing in mixtures. The slope can also change in mixtures, meaning that the interspecific interactions modify the size-density relationship (sometimes called alien-thinning, Harper 1977). Finally, in pure stands, this line can have a bending down to a slope of $-8/3$ for large diameter stands, corresponding to the point where final yield is achieved (West et al. 2009). This bending point might be modified in mixtures, due to niche complementarity, for example (Pretzsch and Forrester, 2017). These changes in MSDR in mixed stands might make questionable the above-mentioned methods based on species-specific maximum densities in monocultures for estimating stand density and species proportion (see also Sect. 2.3), although they can be useful for comparing mixed and pure stands.

Reineke's SDI was initially developed for even-aged monocultures and assumed that the quadratic mean diameter of the stand was an adequate description of the tree-size distribution. Direct application of SDI in mixed stands would require calculating competitive equivalence coefficients for converting SDI of one species to another (Pretzsch 2009) or splitting the index in intra- and interspecific effects (del Río et al. 2014) in a similar way to Curtis (1971) and Long and Daniel (1990), who developed and advocated an additive form of the index (ASDI) for stands with more heterogeneous structures; Woodall et al. (2005) recognized that average wood-specific gravity might be used to predict maximum ASDI for a species mixture. Rivoire and le Moguedec (2012) present an approach for combining ASDI (or similar density measures) into a combined density for a species mixture, when the maximum density of individual species in monoculture is known. Ducey and Knapp (2010) developed an approach for applying ASDI to mixed-species stands, also valid for complex mixtures that include species that do not occur in monocultures. Their formulation preserves the absolute additivity of the density measure and enforces the requirement that the maximum ASDI for one species does not depend on the presence or abundance of other species. They used wood-specific gravity as a functional trait to account for interspecific differences in maximum ASDI, thus avoiding the need to estimate separate parameters for each species. Their formulation has been extended by Ducey et al. (2017) and Bravo-Oviedo et al. (2018) to incorporate additional functional traits, such as shade tolerance, drought tolerance as well as sensitivity to climate.

As an alternative to developing a single density measure for mixtures, Pretzsch et al. (2015) illustrate the use of competition equivalence coefficients for *Pinus sylvestris-Fagus sylvatica* mixtures across Europe (EuMIXFOR Scots pine-beech triplets transect Heym et al. 2017; Ruiz-Peinado et al. 2018). In this approach, the density of one species (as expressed using SDI, ASDI or a similar density measure) is effectively converted into the scale of the density of another species, using the ratio of the maxima of the two density measures. Although competition equivalence coefficients have long been used in ecology (e.g. Lotka 1932; Volterra 1926), their use in describing density of mixed-species stands is relatively new and may provide unforeseen insights, through linkages to a much broader literature on mathematical population and community ecology.

The classical data needed to assess the maximum stand density relationship (MSDR) comes from monitored unthinned permanent plots. If these experiments exist for the species with the highest commercial or ecological interest, they are scarce for mixed-species stands (e.g. Puettmann et al. 1992; Poage et al. 2007; Reyes-Hernández et al. 2013). Recent statistical techniques have been used, such as quantile regression or stochastic frontier analysis, to benefit from temporary plots, particularly National Forest Inventories (Charru et al. 2012; Condés et al. 2017; Vospernik and Sterba 2015). So far, the application to mixed stands is rare but promising (Ducey and Knapp 2010).

2.3 Species Composition and Diversity

Species composition is a key structural characteristic in mixed-species stands, as by definition a mixed stand must be composed of at least two species. Many studies report the relevance of species diversity on forest functioning, including productivity, stability or provision of ecosystem services (e.g. Gamfeldt et al. 2013; Pretzsch et al. 2015; Liang et al. 2016; del Río et al. 2017). However, evidence also exists of the importance of species identities or species composition (e.g. Töigo et al. 2015). At stand level, we may therefore consider both species diversity and species composition to characterize stand structure, although the former might be superfluous in two species mixtures and the later unpractical in systems with a large number of species. Some authors estimate these indicators differentiating between native and non-native tree species, especially when referring to biodiversity (Chirici et al. 2012).

2.3.1 Species Proportion

Of all species composition indicators, species proportion is probably the most frequently used to describe how species occupy growing space at stand level since it is easily estimated, interpreted and applicable in growth and yield studies as well as in forest practice. In mixed-species stands, individuals of two or more species occupy the space above and below ground in often complex spatial arrangements, which may change over time. An appropriate approach to describing species proportions would therefore be to quantify the above- and below-ground resource capture by the sum of individuals per species. In accordance with this approach, Forrester and Albrecht (2014) and Groot et al. (2014) quantified light capture by individuals of each species to study productivity in mixed stands. Forrester et al. (2018), based on data from the EuMIXFOR Scots pine-beech triplet transect (Heym et al. 2017; Ruiz-Peinado et al. 2018), estimated species proportion by leaf area index (LAI) to relate mixing effects to light absorption and stand productivity. However, quantifying resource capture below ground at this scale has not yet been successfully addressed.

Another option is based on quantifying the proportion of the stand area occupied by each species, reducing the n-dimensional growing space (Oliver and Larson 1996, p. 36) into 2D (Sterba 1998; Sterba et al. 2014). While this simplification works well for one-layered stands, it might not be suitable for other stand structures such as stratified mixtures. To define the area occupied by trees of different species, assumptions must be made with regard to the area used by individual trees, since species differ in their resource use efficiency. Most species proportion indices use the ratio of the area occupied by each species (a_i) based on densities relative to species maximum densities. The area these trees would occupy in a fully stocked pure stand is taken as a reference, assuming the maximum density of pure stands as explained in Sect. 2.2, relative to the sum of areas occupied by all species i in the plot ($\sum a_i$), where a_i can be estimated as in Eqs. (2.4) or (2.5) (Waskiewicz et al. 2013; Dirnberger and Sterba 2014; Huber et al. 2014). If $G_{\max}$ is estimated from dominant height (Sterba 1987), it should only be applied in mixtures where dominant height growth is unaffected by the mixture (Huber et al. 2014). The species proportion by area has been found to highly correlate to species proportion estimated from individual tree leaf area (Dirnberger and Sterba 2014; Dirnberger et al. 2017), supporting the suitability of this species proportion definition.

In the past, yield tables have frequently been used as maximum density references for estimating species proportion, although they do not represent the maximum stand density if they are based on thinned stands for the sites analysed (Dirnberger and Sterba 2014). Species-specific maximum density strongly affects the species proportion indicator, so any variation in species-specific maximum density (Fig. 2.1) may change species proportion estimates. Accordingly, errors in species proportion estimates might affect yield comparisons of pure and mixed stands (see Sect. 2.6).

Among the commonly available variables, basal area is most often used to derive species proportions (e.g. Puettmann et al. 1992; Vallet and Perot 2011; Toïgo et al. 2015; Pretzsch 2009; Pretzsch and Forrester 2017). However, using simple ratios between stand level variables without first calculating a_i by species might result in biased species proportions, especially in cases where the maximum density of the species in the mixture differs significantly (Pretzsch 2009, pp. 359–360; Huber et al. 2014; Sterba et al. 2014; Dirnberger et al. 2017). The use of biomass or basal area corrected by species-specific wood density implicitly represents growing space and therefore can be applied to obtain similar species proportions without the estimation of a_i (Assmann 1970; Pretzsch 2009; Pretzsch and Forrester 2017). This method frequently gives similar values to those of basal area to species-specific maximum basal area ratios, while crown projection areas result in larger bias relative to other indices (Pretzsch 2009 pp. 359–360; Dirnberger and Sterba 2014; Huber et al. 2014; Dirnberger et al. 2017). Similarly, additive SDI weighted by species-specific wood density (Woodall et al. 2005; Ducey and Knapp 2010) has been used to express species-specific growing space in mixed stands. However, it has been noted that this approach does not relate actual biomass of the species to their potential biomass but rather assumes equal biomass production of the studied species at a given site. Recent studies reported significant mixing effects on wood density (Zeller et al. 2017), which should be considered when using species-specific wood density to estimate species proportion, although more studies on carbon allocation in mixed vs. monospecific stands are still needed.

For the analysis of changes in species proportions over time, the statistical peculiarities of compositional data need to be accounted for (Kobal et al. 2017). Changes in maximum density references and total stand density over time add to the complexity of these analyses.

2.3.2 Species Diversity

A number of indices to characterize community species diversity have been developed. These are also commonly applied to mixed-species stands (Table 2.1). Species richness only considers the number of species, providing scarce information on species' dominance. However, it is often used when analysing the relationship between diversity and productivity in forests (e.g. Vilà et al. 2007; Belote et al. 2011; Gamfeldt et al. 2013). This relationship can be affected by the covariation of the tree species number with variables like stand age, successional stage and/or site variables (Vilà et al. 2005, 2007; Vallet and Perot 2011). The evenness index (Magurran 1988) considers growing space partitioning among species and provides an indicator of the homogeneity in species abundance (proportion). The evenness index takes the maximum value of 1 when the species have equal abundance in the stand and are not defined in monospecific stands. Species evenness was found to explain forest productivity together with species richness in the global meta-analysis of Zhang et al. (2012). However, only a few other studies have analysed the influence of species evenness and richness on stand growth or productivity (Liang et al. 2007; Szwagrzyk and Gazda 2007; Lei et al. 2009; Silva Pedro et al. 2017). The Shannon-Weaver index (Shannon 1948) and the Simpson diversity index (Simpson 1949) consider both species richness and frequencies, increasing their values with the number of species and when the trees are distributed equally among all the species. Therefore, they are usually preferred to describe species diversity, although they have scarcely been used to study the species diversity effect on productivity (e.g. Zhong et al. 2017). Some other studies consider functional diversity instead of species diversity, since species with similar functional traits may occupy the same niche and therefore show similar behaviour (functional redundancy de Bello et al. 2007). However, even small differences in functional traits between species can trigger significant mixing effects on productivity (Riofrío et al. 2017).

Table 2.1 Indices for characterizing species richness and diversity

Equation	Description
Simpson Diversity Index (*1-D*) (Simpson 1949): $D = 1 - \frac{\sum_{i=1}^{R} ni(ni-1)}{N(N-1)}$	The Simpson index was introduced in 1949 by Edward H. Simpson to measure the degree of concentration when individuals are classified into types. Simpson's diversity index (1-D) is a simple mathematical measure that characterizes species diversity in a community. It takes into account the number of species present, as well as the abundance of each species; ni is the number of entities belonging to the ith type, and N is the total number of entities in the dataset. R is richness (the total number of types in the dataset)
	Range: 0–1; the greater the value, the greater the sample diversity. The index represents the probability that two individuals randomly selected from a sample will belong to different species. High scores (close to 1) indicate high diversity. Low scores (close to 0) indicate low diversity
Shannon Index (H') (Shannon 1948): $H' = -\sum_{i=1}^{s} p_i \ln p_i$	The Shannon index (H') was developed to characterize the species diversity in a community. Like Simpson's index, Shannon's index accounts for both abundance and evenness of the species present. p is the proportion (n/N) of individuals of one particular species found (n) divided by the total number of individuals found (N). The proportion of species i relative to the total number of species (p_i) is calculated and then multiplied by the natural logarithm of this proportion (lnp_i). S is the number of species
	Range: 0 to ln(S). When all species in the dataset of interest are equally common, all pi values equal 1/S, and the Shannon index hence takes the value ln(S). If practically all abundance is concentrated in one species, and the other species are very rare (even if there are many of them), it approaches 0. When there is only one species in the dataset, Shannon entropy exactly equals 0
Berger-Parker Index (D) (Berger and Parker 1970) $D = \frac{N_{\max}}{N}$	It is a simple measure of the numerical importance of the most abundant species. The Berger-Parker index is an analytical relationship with the geometric series of the species abundance model and reports the proportional abundance of only the most abundant species in the population. N_{max} is the number of individuals in the most abundant species, and N is the total number of individuals in the sample
	The reciprocal of the index, 1/D, is often used, so that an increase in the value of the index accompanies an increase in diversity and a reduction in dominance
Evenness Index (E) (Pielou 1975) $E = \frac{H'}{\ln S}$	Species evenness refers to how close in numbers each species in an environment are. In the evenness index (E), H' is the number derived from the Shannon diversity index and $H'_{\max}$ is the maximum possible value of H' (if every species was equally likely). Some indices, called heterogeneity indices by PEET (1974), incorporate both aspects, but HElP (1974) made the point that in order to be useful, an evenness index should be independent of a measure of species richness
	Range: 0–1, with 1 being complete evenness. H' by $H'_{\max}$ (here $H'_{\max} = \ln S$). The less the evenness in communities between the species (and the presence of a dominant species), the lower E will be. And vice versa

(continued)

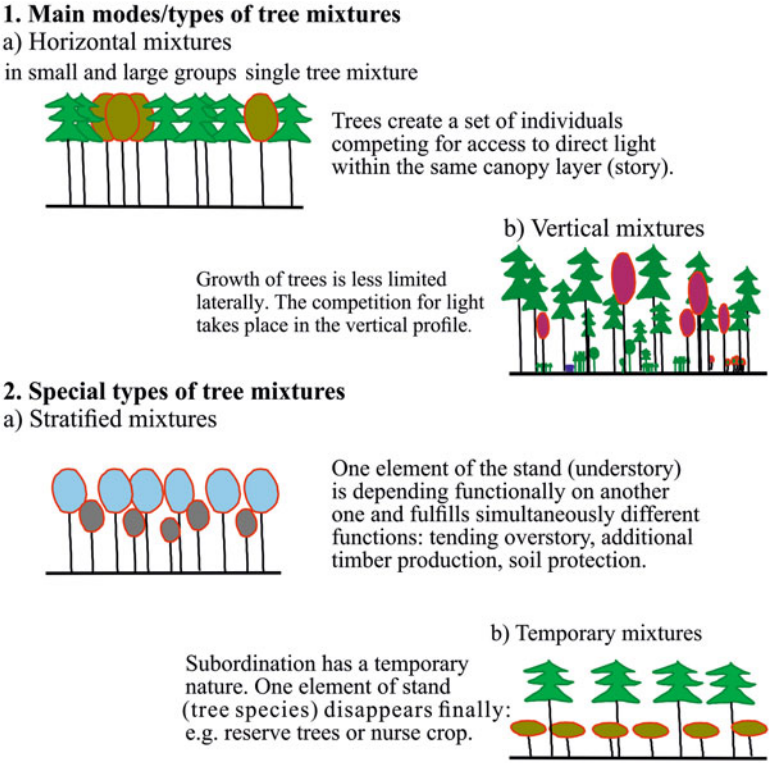
Table 2.1 (continued)

Equation	Description
Fidelity Measure (u) (Bruelheide 1995, 2000) $u = (n_p - \mu)/\sigma$	Bruelheide (1995, 2000) proposed the fidelity measure u, which compares the observed number of occurrences of the species in the vegetation unit (n_p) with the expected number of occurrences ($\mu = n\ Np/N$). The u value is defined as the deviation of the observed frequency of the species occurrence in the vegetation unit from the expected frequency, compared with the standard deviation (σ). n is number of species occurrences in the entire data set; N is number of relevés in the data set; Np is number of relevés in the vegetation unit

2.4 Tree Distribution Pattern

Trees in mixed forests create different horizontal and vertical distribution patterns depending on their ecological traits (degree of association, growth rate, shade tolerance, nutrient and water supply) as well as site conditions (Getzin et al. 2006; Pretzsch et al. 2016) and applied silvicultural systems (Smith 1986). It makes little sense to separate vertical and horizontal structural components, as they are functionally related and affect each other (Fig. 2.2). For instance, adding a new species can create a new canopy layer due to differences in growth rates between species. Furthermore, the degree of horizontal structural diversity can change with vertical position in a stand (Brokaw and Lent 1999). For example, in eutrophic Bialowieza primeval forests, the understory is homogeneous and monospecific, while the overstorey can be very heterogeneous and composed of at least five species (Bielak and Brzeziecki 2017).

Horizontal and vertical tree distribution patterns affect the main processes in forest stand dynamics by modifying the supply, capture and efficiency of resource use and therefore the intra- and interspecific interactions. The increasing heterogeneity of horizontal and vertical stand structure is strongly linked to a higher number of species (Pommerening, 2002; Scherer-Lorenzen et al. 2005). For a given species composition, the stand dynamics can also differ substantially depending on the type of spatial species intermingling, as this will determine whether intra- or interspecific competition is the prevalent interaction between trees and, consequently, to what extent mixing effects can be expected (Pretzsch 2009, pp. 227–229). Interactions and patterns between tree species are more often studied above ground than below ground. However, recent research results suggest that niche partitioning and vertical stratification of root systems take place as well (Fölster et al. 1991; Brown 1992), although this is not always the case (Meinen et al. 2009). In this section, firstly we present the set of measures, indices and methods for characterization of horizontal tree distribution patterns, including spatial patterns and tree species intermingling, and secondly, we describe vertical tree distribution patterns together with species-specific height growth and canopy space partitioning in mixed versus monospecific forests.



Trees create a set of individuals competing for access to direct light within the same canopy layer (story).

Growth of trees is less limited laterally. The competition for light takes place in the vertical profile.

One element of the stand (understory) is depending functionally on another one and fulfills simultaneously different functions: tending overstory, additional timber production, soil protection.

Subordination has a temporary nature. One element of stand (tree species) disappears finally: e.g. reserve trees or nurse crop.

Fig. 2.2 Types of tree species mixtures characterized by different spatial and temporal effects. (Adapted from Schütz 2001)

2.4.1 Horizontal Spatial Pattern

The horizontal spatial pattern of trees is an important attribute of stand structure, which provides an idea of the variation in tree spacing rather than stand density, which represents its average (McElhinny et al. 2005). The variation in spacing is frequently described by an aggregation index, which quantifies the degree of clustering in the horizontal arrangement of trees (McElhinny et al. 2005). Three main types of spatial pattern can be defined as (1) regular, (2) random (Poisson) and (3) clumped (aggregated) in varying degrees, depending, in natural forests, on site, species composition, sampling scale and stand age (Szwagrzyk and Czerwczak 1993; Hanewinkel 2004; von Oheimb et al. 2005; Paluch 2007). There are different approaches to study the spatial distribution of trees, with a large number of available methods and indices described in the literature (e.g. Dale 1999; Pretzsch 2009; Gadow et al. 2012).

Methods that use tree positions are often classified as tree-based and point-based approaches (Gadow and Hui 2002; Pretzsch 2009, p. 246) depending on the used distances (between trees or between point and trees). Some methods provide detailed information about changes in spatial patterns at different scales. They depend on a distance variable, r, and quantify correlations between all pairs of trees within a distance of approximately r between them. This allows these methods to be related to various ecological scales and also, to a certain degree, to account for long-range point interactions (Pommerening 2002). The most common and traditional second-order characteristic is the Ripley's K-function (Ripley 1977) or its transformed form, i.e. the L-function (Besag 1977) (Table 2.2). As cumulative functions like L and K are not always easy to interpret, functions using derivates are often preferred for detailed structural analysis. One of these is the pair correlation function, $g(r)$, which is related to the first derivative of the K-function according to the interpoint distance r (see Illian et al. 2008). The second-order characteristics are recommended for analysing spatial patterns if mapped data in larger observation windows with more than 100 points are available (Pommerening and Stoyan 2006).

As the previous methods do not provide an index or mean value at stand level, another approach is to use simple methods such as the commonly used Clark and Evan's aggregation index (Clark and Evans 1954) or Pielou's distribution index (Pielou 1959) (Table 2.2). These indices can be easily integrated into any analysis, even in the case of small spatial observation windows like circular plots, frequently used in National Forest Inventories.

Indices based on distances provide a good estimation of spatial pattern, although in some cases it is not possible to measure tree positions. There are certain indices based on angle-based measures among neighbours (Gadow et al. 2012, pp. 43–46), such as the uniform angle index (W) (Gadow et al. 1998; Gadow and Hui 2002), but their possible advantage over distance-based methods when measuring is highly questionable. Although the use of W may provide information on the mean spatial symmetry of competition (Gadow et al. 1998), it requires angle measurements (or at least classification) among trees. This is not only costly but also provides no real tree coordinates which can be further used for another spatial structure.

Other indices are based on local densities measured in sample quadrants (Pretzsch 2009, pp. 252–255), which can be useful for studying seedling and sapling distribution. The variance-mean ratio proposed by Clapham (1936) or Morisita's index of dispersion developed by Morisita (1959) in particular has proven to be useful in forest research (Pretzsch 2009). Cox (1971), David and Moore (1954), Loetsch (1973) and Douglas (1975) describe similar indices. Their main advantages are that stem coordinates are not required and that they provide an estimate of local density variation. However, the main constraint is that they depend heavily on the sample quadrat size. Many authors suggest that the sample quadrat size should be selected so that between one and four objects are present, on average, in each sample quadrat (Pretzsch 2009). Therefore, quadrats between 1×1 m and 5×5 m are used, the smaller ones being used for natural regeneration at seedling stage, while the larger ones are used at sapling stage.

Table 2.2 Overview of the most common functions and indices for depicting the horizontal spatial pattern

Equation	Description
L-function (Besag 1977): $L(r) = \sqrt{\frac{K(r)}{\pi}}$, for $r \geq 0$ $K(r) = \frac{1}{\lambda} \times \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{P_{ij}(r)}{n-1}$, with $P_{ij}(r) = \begin{cases} 1 \text{ if } r_{ij} \leq r \\ 0 \text{ if } r_{ij} > r \end{cases}$	*L*-function is a transformed version of *K*-function ($K(r)$) by Ripley (1977), dividing it by π and taking the square root of the quotient. *r* denotes radius centred at the typical point *i* (tree) of the point pattern, where *xxxxxx* is the mean density in the observation window. The *L*-function is often used for testing the complete spatial randomness hypothesis, e.g. in Ripley's *L*-test (Dixon 2002). The functions identify the extent to which the tree distribution pattern is more or less dense than the Poisson distribution as the distance r from the tree base increases
	Range: cumulative function changing over the radius considered
Aggregation Index *R* (Clark and Evans 1954): $R = \frac{\bar{r}_{\text{observed}}}{E(r)}$, $E(r) = 0.5 \times \sqrt{\frac{A}{N}}$	*R* describes the horizontal tree distribution pattern by relating the observed arithmetic mean of distance between reference trees and neighbours ($\bar{r}_{\text{observed}}$) to the average distance to be expected when trees are randomly distributed ($E(r)$). *N* is the total number of trees in the plot, and *A* is its area. The edge effect arising from the spatial limitations of experimental plots can be minimized by applying the boundary correction factor by Donnelly (1978)
	Range: 0–2.1491. Values below 1 show a tendency towards clustering, while those around 1 indicate random distribution and those above 1 reveal a tendency towards regular distribution
Uniform Angle Index (*W*) (Gadow et al. 1998): $W_i = \frac{1}{n} \sum_{j=1}^{n} v_j$ where $v_j = \begin{cases} 1, & \alpha_j < \alpha_0 \\ 0, & \text{otherwise} \end{cases}$	*W* defines the degree of regularity of the spatial distribution of tree position based on angles between trees instead of radius. Assuming complete regularity of the positions of the *n* nearest neighbours around reference tree *i,* the expected standard angle α_0 between reference tree and neighbour would equal to 360°/*n*. For instance, in case of four neighbours, $\alpha_0 = 90°$ and thus five possible values of *W* can be expected (0; 0.25; 0.5; 0.75; 1.0)
	Range: 0–1. Values below 0.5 indicate regular tree distribution pattern, while those between 0.5 and 0.6 can be classified as random distribution and those greater than 0.6 can be considered as clumped

2.4.2 Species Intermingling

The mingling pattern is the result of multidimensional relationships of various factors influencing horizontal spatial distribution in mixed-species stands and varies from a tree-to-tree intermingled pattern to pronounced segregation. The first classification of mingling patterns was presented by Langhammer (1971) who distinguished three main categories: stem-wise (tree-to-tree, intimate), row-wise and group-wise patterns. Row-wise patterns can be used as a single row or multiple rows (strip-wise). Group-wise patterns are most common in natural forests, where regeneration occurs in canopy gaps (Madsen and Hahn 2008; Nagel and Svoboda 2008). They can be defined depending on the size of the groups, which can range from 0.05 ha (several seedlings) to 0.5 ha.

To quantify species intermingling patterns, a number of indices were elaborated which allow comparative studies of different stands. One of the most commonly used worldwide in ecological studies is the segregation index by Pielou (S) (Pielou 1977). This index is based on the nearest-neighbour method (Table 2.3), and its main advantage is that it is easily interpreted, although some effort is required to measure tree coordinates. In stands where there are more than two species, S can be calculated for each species separately, providing the mingling pattern of the target species (Fig. 2.3a).

The other mingling indices are based on the species intermingling M proposed by Gadow (1993), which quantifies the proportion of neighbours of another species, providing a tree-level value that can be averaged at both species and stand level (Fig. 2.3 and Table 2.3). The mean value of species intermingling can be compared to the expected mingling (Lewandowski and Pommerening 1997). In theory the coordinates are not necessary to compute this index as the registration of neighbour species identity is sufficient (Hui et al. 2011), although it also requires the n nearest neighbours to be identified. Therefore, in practice, the calculation is usually performed based on a dataset that includes tree positions. One disadvantage of this index may also be the fact that it does not consider the number of species. In turn, the spatial diversity status MS_i combines M with the species richness, which gives the species average spatial status $\mathrm{MS}_{\mathrm{sp}}$ when averaged per species, and the tree species spatial diversity TSS when averaged per stand (Gadow et al. 2012, pp. 57–62).

Several studies consider the influence of horizontal spatial distribution and species intermingling on stand growth in mixtures using distance-dependent individual tree modelling approaches (Pretzsch 1995a; Ngo Bieng et al. 2013; Rötzer 2013). However, scarce research has been conducted to date based on empirical data. Pretzsch et al. (2012a) compared the stand growth in pure and mixed stands with two intermingling patterns, reporting overyielding or higher productivity in mixed stands only when there was a tree-wise pattern.

Table 2.3 Overview of the most commonly used indices for characterization of species intermingling

Equation	Description
Segregation Index (S) (Pielou 1977) $S = 1 - \frac{p_{ij}}{E(p_{ij})}$	S describes the degree of mixing of trees of two species A and B in a forest based on the nearest-neighbour tree distances. S considers the ratio of the observed probability (p_{ij}) that the reference tree i and its nearest neighbour j belong to different species along with the same probability for completely randomly distributed or independent species attributes. If all neighbours are of different species $S = -1$, while $S = 1$ means that the reference tree is surrounded by the same species
	Range: -1 to 1. Values greater than 0 indicate a trend towards segregation; values below 0 indicate a trend towards association. Independent distribution of species is indicated by values near 0
Mingling Index (M) (Füldner 1995): $M_i = \frac{1}{n}\sum_{j=1}^{n} v_j$ $v_j = \begin{cases} 1, & \text{spec}_i \neq \text{spec}_j \\ 0, \text{otherwise} \end{cases}$	M is a single-tree variable and gives the proportion of the n nearest neighbours j ($j = 1 \ldots n$) of the i reference tree which do not belong to the same species as the reference tree i. In case of $n = 3$ neighbours M can take the values 0, 0.33, 0.67or 1.0. The distribution and mean M allows evaluating the intermingling
	Range: 0–1. The higher the value of M, the more the tree species are intermingled. Low values indicate stands with large groups of only one tree species and therefore segregation
The Spatial Diversity Status (MS) (Gadow and Hui 2002): $MS_i = \frac{S_i}{n_{\max}} \times M_i$	MS is an improvement on the mingling index. MS of a particular tree species is determined by the relative species richness within the stand or analysed spatial unit i and the degree of mingling of the reference tree. S_i is the number of tree species in the neighbourhood of the reference tree i, including tree i, and $n_{\max}$ is the maximum number of species in the structure unit i. MS is especially sensitive to rare tree species. One practical advantage in terms of the assessment effort required is the fact that, as in the case of M, it is not necessary to measure tree coordinates in the field
	Range: 0–1. A reference tree of a common species is more likely to have neighbours of the same species, which is reflected by low MS_i values. On the other hand, a rare species is likely to produce a high proportion of high MS values

2.4.3 Vertical Spatial Pattern

The vertical stand structure in mixed stands is the spatial arrangement of different tree species along the vertical axis. The vertical distribution of tree species changes over the stand development through growth and mortality, as well as natural disturbances and silvicultural interventions (Latham et al. 1998; Oliver et al. 1999). The traditional approach of hand drawings of vertical stand profiles or photographs has frequently been presented for primeval forests (Faliński 1986; Koop 1989; Peterken 1996). However, these methods are not based on measurements and therefore only provide a qualitative overview. A more advanced and complete description of vertical structure requires the spatial positions of the trees to be recorded along with their size and species. Nowadays, tree position and size can

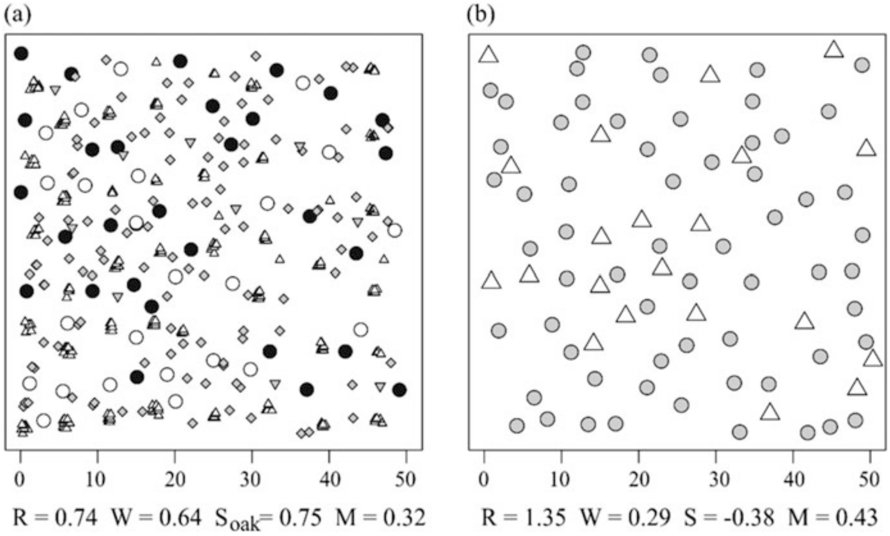


Fig. 2.3 Quantification of the horizontal tree spatial pattern (*R* and *W*) and species intermingling (*S* and *M*) in experimental plots: (**a**) 19-year-old group-wise mixed stand established by applying the Polish group planting method for *Quercus robur* L. (triangle), with admixture of planted *Larix decidua* Mill. (circle), as well as *Betula pendula* Roth. (filled circle), *Carpinus betulus* L. (rhombus) and *Acer pseudoplatanus* L. (inverse triangle) from natural regeneration (North-Eastern Poland); (**b**) 72-year-old tree-wise mixed stand of *Pinus sylvestris* L. (grey circle) and *Quercus petraea* (Matt.) Liebl. (triangle) (Central Poland)

be recorded using LIDAR survey techniques (Wang et al. 2008). Based on information on coordinates of the trees, their diameters at breast height and at least some of the heights, 3D visualization can be generated using forest models such as SILVA (Pretzsch et al. 2002), BWINPro (Nagel and Schmidt 2006) or MOSES (Hasenauer 1994).

Tree height is obviously a particularly important size variable, which can be used to describe the vertical structure of the stand (Temesgen and Gadow 2004; McElhinny et al. 2005). If all tree heights are known, frequency histograms can show the distribution of stem density, basal area, biomass, LAI, etc. for each tree species separately within defined height classes (Brokaw and Lent 1999; Parker and Brown 2000; Bongers 2001). Descriptive statistics of these height distributions can be used in stand level analyses in the same way as diameter distributions (Sect. 2.5). Similarly, mean height together with standard deviation or variation in tree height can be used as a straightforward index to assess vertical structure (Barbeito et al. 2009).

Another approach uses distance-independent or distance-dependent structural indices (Table 2.4). Based on the principle of the nonspatial diversity index *H* by Shannon (1948), different authors have proposed specific measures to describe vertical differentiation. MacArthur and MacArthur (1961) calculated foliage height diversity (*FHD*), based on the proportion of leaf area within various height intervals

Table 2.4 Overview of indices for characterization of the vertical spatial pattern

Equation	Description
Vertical Species Profile *A*	*A* is based on the common diversity index H by Shannon (1948). In addition, index *A* takes into account the presence of each species in different tree height zones. *S*, number of species in the stand; *Z*, number of height zones (three in this case); $p_{ij} = n_{ij}/N$, species proportions in the zones,; n_{ij}, frequency of species *i* in zone *j*; *N*, total number of individuals. Standardization of *A* can be done by dividing *A* value by the maximum value of the *A* index, i.e. $A_{\max} = \ln(S \times Z)$
(Pretzsch 1995b):	
$A = -\sum_{i=1}^{S}\sum_{j=1}^{Z} p_{ij} \times \ln p_{ij}$	
	Range: ≥ 0 (0 for a single-layered pure stand). The more heterogeneous the vertical profile, the higher A becomes
Height Differentiation Index (*TH*)	*TH* measures small-scale variability in the height size for the *i* reference tree and its *n* nearest neighbours *j* ($j = 1 \ldots n$); frequently $n = 3$ is used. The average value of *TH* for a whole stand or each tree species (subpopulation) can be calculated. *TH* values are summed and divided by the number of trees or individuals of the subpopulation. Based on defined classes of *TH*, the frequency histogram by each tree species can be elaborated
(Gadow 1993):	
$\mathrm{TH}_{ij} = 1 - \frac{\mathrm{MIN}(H_i,\ H_j)}{\mathrm{MAX}(H_i,\ H_j)}$	
	Range: 0–1. (0 means that neighbouring trees have an equal height, whereas values close to 1 reflect high differentiation)
Structural Complexity Index (SCI)	*SCI* is the sum of the surface areas of triangulated irregular network in $x{-}y{-}z$ space divided by the projected ground area of all triangles in the $x{-}y$ space. *x, y* are the coordinates of a particular tree, while *z* indicates its height. Subscripts *a, b* and *c* are trees within a triangle *i*, *n* is the number of nonoverlapping triangles in the sample plot, and *SCI* is the product of the vectors *AB* and *AC*
(Zenner and Hibbs 2000):	
$\mathrm{SCI} = \sum_{i=1}^{n} \frac{1}{2} \times \frac{\left\lvert \begin{bmatrix} x_b - x_a \\ y_b - y_a \\ z_b - z_a \end{bmatrix}_i \times \begin{bmatrix} x_c - x_a \\ y_c - y_a \\ z_c - z_a \end{bmatrix}_i \right\rvert}{\left\lvert \begin{bmatrix} x_b - x_a \\ y_b - y_a \end{bmatrix}_i \times \begin{bmatrix} x_c - x_a \\ y_c - y_a \end{bmatrix}_i \right\rvert}$	
	Range: ≥1 (1 when all trees are the same size, regardless of spatial pattern; no upper bound). Measure of both horizontal and vertical structure

above ground. As the estimation of leaf area is very time-consuming, *FHD* is often replaced by tree height diversity (*THD*) based on the proportion of trees in each height layer (Kuuluvainen et al. 1996). While the above indices provide a good estimation of vertical canopy distribution and are correlated well to habitat functions, they do not take into consideration the species composition. Thus, Pretzsch (1995b) proposed the differentiation of tree species within three layers, following the classification proposed by Assmann (1970), i.e. 100–80%, 80–50% and 50–0% of the

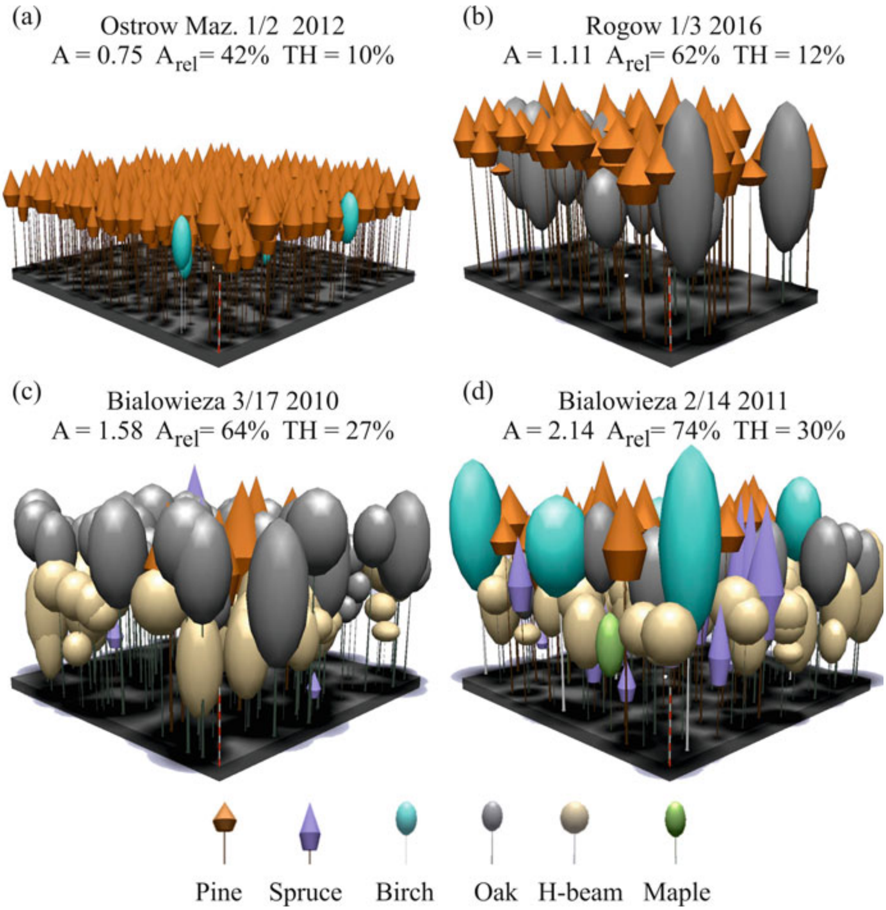


Fig. 2.4 Quantification of the vertical stand structure in long-term experimental plots near Ostrow Mazowiecka, Rogow and Bialowieza (Poland) according to the absolute and standardized values of the vertical species profile index (A and A_{rel}), as well as the height differentiation index (TH): (**a**) 40-year-old, monolayered stand of *Pinus sylvestris* L. with single admixture of *Betula pendula* Roth.; (**b**) 72-year-old almost monolayered stand of *Pinus sylvestris* L. and *Quercus petraea* (Matt.) Liebl.; (**c**) 85-year-old two-layered mixed stand of *Quercus robur* L., *Pinus sylvestris L.*, *Picea abies* (L.) Karst and *Carpinus betulus* L.; and (**d**) ~82-year-old multilayered diverse tree species mixed stand of *Quercus robur* L., *Pinus sylvestris L.*, *Picea abies* (L.) Karst, *Betula pendula* Roth., *Acer platanoides* L. and *Carpinus betulus* L

maximum height (Fig. 2.4), the vertical species profile (A). The standardised species profile index (A_{rel}) standardizes A taking into account the number of species and the number of considered layers (Pretzsch 2009, pp. 282–283). Index A has the advantage that it does not require information on the horizontal distribution while providing information on vertical distribution of species. Staudhammer and LeMay (2001) proposed the use of basal area instead of tree numbers for calculating the proportion of species corresponding to each layer. Two distance-dependent indices that can also be used to assess vertical differentiation are the height differentiation index (TH) (Gadow 1993) and the structural complexity index (SCI) proposed by Zenner and Hibbs (2000) and Zenner et al. (2015) (Table 2.4).

Only a few studies have included the analysis of vertical structure in mixed vs. pure comparisons (Menalled et al. 1998; Pretzsch et al. 2016) or its effect on diversity-productivity relationships (Edgar and Burk 2001; Lei et al. 2009; Riofrío et al. 2017). Some competition indices include the effect of the vertical distribution of crowns (Biging and Dobbertin 1992; Pretzsch et al. 2002), and therefore vertical structure is considered when using such indices in forest modelling. However, a more in-depth analysis of the effect of the vertical distribution of species on forest functioning at stand level is needed (Pretzsch et al. 2016), since certain mechanisms related to overyielding may be linked to vertical canopy structuring (Forrester et al. 2018).

2.4.4 Species-Specific Height Growth and Canopy Space Partitioning

According to Leikola (1999), who adopted Langhammer's (1971) classification, mixed forests in the strictest sense comprise trees belonging to the same storey (Fig. 2.2). However, mixed-species stands are often stratified in height by species due to differences in height growth patterns, maximum heights and shade tolerance characteristics (Larson 1992; Peterken 1996; Schütz 1999). Stratification is a dynamic process and can be temporary, i.e. one tree species disappears, for example, in managed forests, reserve trees or nurse crop (Fig. 2.2). Where species are tolerant enough to survive in the understory, the stand can consist of more than two crown strata (Smith, 1986; Oliver and Larson 1996). A shift in height dominance from one species to another is a common phenomenon in mixed forests (Larson 1992). Furthermore, differences in age between individuals in the stand can also be a major factor in either the maintenance of, or shift in, height dominance between species and canopy space partitioning (Larson 1992; Kelty 1992). Vertical stratification of the canopy often becomes more pronounced with increasing age (Larson 1992; Oliver and Larson 1996; Pretzsch 2005).

The height growth curves are species-specific, with distinct differences in the sigmoid height growth curves of early-successional and light-demanding (e.g. *Betula*, *Larix*, *Pinus*), late-successional and shade-tolerant (*Abies*, *Fagus*, *Picea*) as well as intermediary species (*Acer*, *Tilia*, *Fraxinus*) (Assmann 1970, 44–45). The species-specific levels of the height curves in monospecific stands and the age of intersection may reveal the height and light competition to be expected when tree species are mixed (Fig. 2.5a). However, while in pure even-aged stands, intraspecific competition only has a minor effect on the dominant height development; interspecific competition can considerably modify species-specific

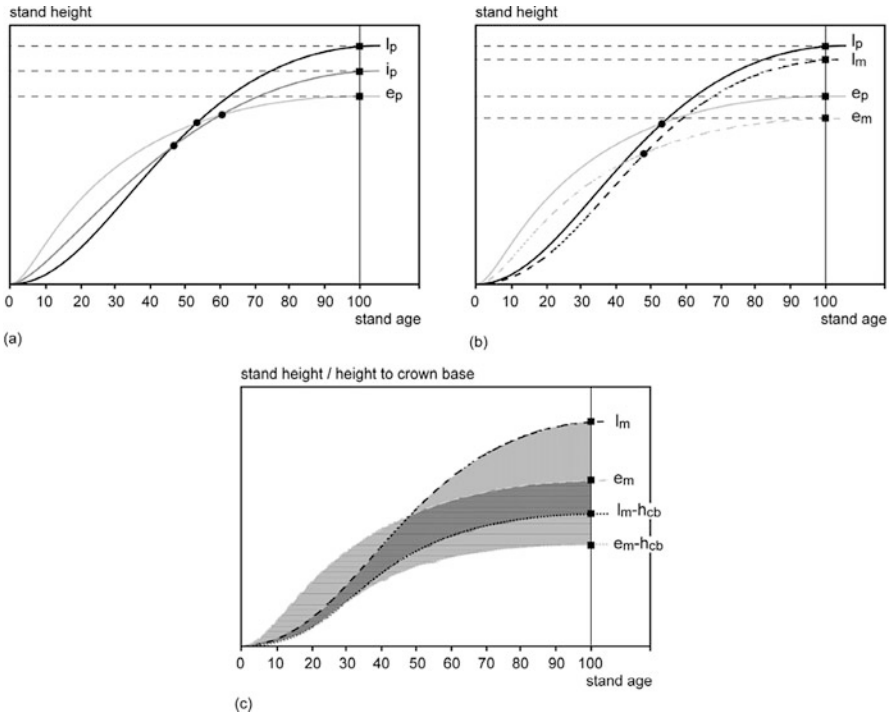


Fig. 2.5 Course of species-specific height and height to crown base provide key information on the dynamics of mixed-species stands. Schematic representation of (**a**) sigmoid height growth in pure stands (p) for early-successional (e_p), intermediate (i_p) and late-successional tree species (l_p); (**b**) delayed height growth by interspecific competition in mixed-species stands; and (**c**) ingrowth of the late-successional and shade-tolerant species (l_m) into the crown layer of the early successional species (e_m). h_{cb} is height to the crown base

growth patterns, especially when species with very different height growth dynamics are mixed. Figure 2.5b shows delayed height growth of both mixed species (Wiedemann 1951, pp. 131–133). However, these changes in species-specific height growth in mixed stands can vary significantly with stand density (Amoroso and Turnblom 2006; Garber and Maguire 2004). The leading species commonly reduces the growth of the lower species by pre-empting the light, while the lower species may reduce the growth of the leading species by using limited below-ground resources and by entering and reducing their crown space from below (Knapp 1991) (double-hatched area in Fig. 2.5c). The point of intersection of the height curves of the two species in a mixture indicates the stand age at which the previously suppressed species may begin to dominate (Fig. 2.5b). Therefore, the ratio of mean heights between species at a given stage is a simple and effective indicator for considering species stratification over the development of the stand (Edgar and Burk 2001; Bielak et al. 2014).

2.5 Tree-Size Distribution and Growth Partitioning Among Trees

Tree-size distribution can be understood as an emergent property, i.e. a property that emerges from the demographics and dynamics of individuals influenced by the tree distribution pattern and, therefore, represents an intermediate scale between tree and stand levels. Tree size directly relates to the stage of development of the stand, to age structure and to the competition among trees that can occur at intraspecific level or as a consequence of competitive advantage or disadvantage of one of the species within the mixture at interspecific level. In this section we describe the way in which tree-size distribution, growth partitioning among trees of different sizes and age structure in mixed forest stands can be characterized.

2.5.1 Tree-Size Distribution

The simplest way to describe the size distribution of a mixed forest for a given point in time is through the use of stand tables displaying the number of trees, basal area or volume per species and diameter classes, parameters commonly collected in forest inventories (Dieler et al. 2017). Although approaches based on diameter classes have some inherent weaknesses, they provide useful information on stand structure for modelling and understanding long-term forest dynamics. However, in order to use this information at stand level, size distributions must be described according to their main attributes.

Basic statistics of distributions such as minimum, mean, maximum, standard deviation, skewness or kurtosis have been used to study the effect of mixing on size distribution dynamics (Pretzsch and Schütze 2014, 2015). The use of these descriptive statistics has the advantage of not requiring costly information on the spatial distribution of the trees. These statistics can be evaluated by species for different tree attributes. A stand-level value can easily be calculated as a weighted mean according to the proportions of the species. This method takes into account the species-specific mean tree size as well as their occupancy, although it depends on the definition of species proportion (see “Species diversity and composition” section).

The most common approaches to describe tree-size distributions include the use of a diameter distribution model based on probability density functions (e.g. the Weibull or Johnson-S_B functions) for each species. The diameter frequency data of mixed-species stands, unlike pure stands, may present highly irregular shapes, including multimodes (Fig. 2.6). Therefore, the use of unimodal statistical distributions when attempting to apply distribution models can lead to oversimplified descriptions of stand structure (Maltamo 1997). One option to avoid this limitation is the use of a “mixture” distribution or finite mixture model (FMM), which considers a frequency distribution made up of two or more component distributions. FMM was introduced by Liu et al. (2002) to characterize diameter distributions in mixed stands. The FMM models provide a useful tool for effectively describing

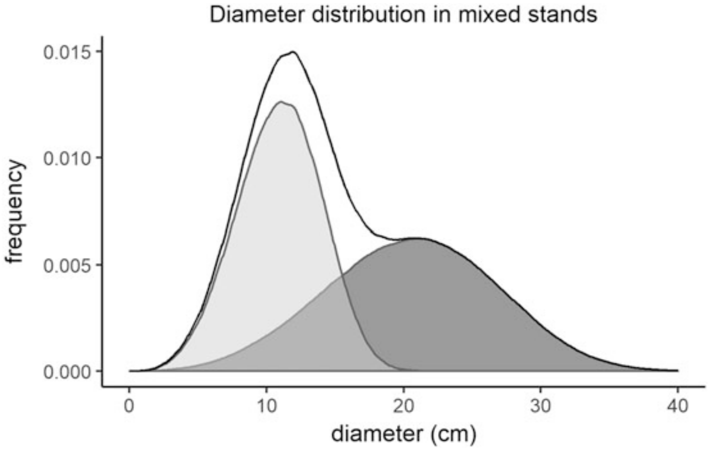


Fig. 2.6 Diameter distribution of a mixed stand of Scots pine (dark grey), European beech (light grey) and total for one of the EuMIXFOR-triplets (Heym et al. 2017)

mixed-species stands, as these models are more flexible for describing highly skewed and irregular diameter distributions for the whole plot, while providing an acceptable estimation for each species component as well as the mixture proportions (Liu et al. 2014; Podlaski and Roesch 2014; Pach and Podlaski 2015). Distribution-free methods have also been proposed to describe multimodal distributions such as percentile prediction (Borders et al. 1987), or nonparametric statistical methods (Droessler and Burk 1989; Haara et al. 1997) such us k-nearest-neighbour regression (Maltamo and Kangas 1998).

In addition to size distributions, size heterogeneity can be described by indices, e.g. the size differentiation index proposed by Füldner (1995), the Gini coefficient (de Camino 1976) or the Shannon index applied to tree sizes (Shannon 1948). The size differentiation index (TM) (Eq. 2.7) is a measure of the relative size differences among neighbouring trees presenting the advantage of not requiring tree coordinate spatial information. Stands with small diameter differentiation have index values near 0, while stands with higher differentiation tend towards a value of 1. However, this index has two major problems, one being the need to register the size of the neighbours and the other that it does not consider the species composition (Pretzsch and Schütze 2014), which reduces the value of the index for characterizing structure in mixed stands:

$$\mathrm{TM}_i = \frac{1}{n}\sum_{j=1}^{n}\left(1 - d_{ij}\right) \tag{2.7}$$

where

TM_i is the size differentiation index for tree i.

n is the number of trees in the sample plot.

d_{ij} is the relation between the thinner and thicker dbh of the analysed neighbouring pair. Diameter is a commonly used attribute, but others could be used.

The Gini coefficient (GC) (Eq. 2.8) also ranges from 0 (very homogenous distribution) to 1 (maximum inequality), which can be represented through the Lorenz curve (de Camino 1976). It can be used for quantifying the inequality in size or growth between the trees in the stand:

$$\mathrm{GC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\left|x_i - x_j\right|}{2n(n-1)\bar{x}} \tag{2.8}$$

where

GC is the Gini coefficient.
n is the number of trees in the sample plot.
x_j and x_j are the dbh for the ith and the jth tree in the stand with $1,\ldots n$ trees in the stand.

These indices have been employed to relate size heterogeneity to stand dynamics (Varga et al. 2005; Liang et al. 2007; Lei et al. 2009; Pommerening et al. 2016; Pretzsch et al. 2016).

2.5.2 Growth Partitioning Among Trees of Different Sizes

A crucial characteristic of stand dynamics, strongly influenced by stand structure, is that stand growth involves trees of different sizes (Pretzsch 2018). The growth partitioning among trees of different size is linked to the mode of competition, i.e. the degree of size asymmetry. According to Weiner (1990), competition for light is mainly size-asymmetric, while competition for below-ground resources is generally size-symmetric, and therefore the site conditions influence the degree of size asymmetry (Pretzsch and Biber 2010). In pure stands, growth partitioning among trees of different sizes is often size-asymmetric, as the tallest trees in fully stocked middle-aged stands can pre-empt light and grow overproportionally due to their superior height and therefore greater access to light (Schwinning and Weiner 1998; Hara 1992, 1993). As mixing can modify above-ground and below-ground resource use, it can have an important effect on the distribution of growth between the trees in a stand (see also 2.4.4) and therefore on the mode of competition (Hara 1992, 1993; Pretzsch and Schütze 2014, 2015; del Río et al. 2014).

The way in which the growth in a stand is distributed among trees of different sizes can be characterized by the relationship between the cumulative tree volume growth and cumulative tree volume (Binkley 2004; Binkley et al. 2006). Mixing may modify the growth distribution among trees of different sizes due to more similar growth efficiency of dominant and understorey trees (Fig. 2.7). Beyond the graphical representation, the course of the curve can be characterized by the difference in the Gini coefficients for cumulative growth and the Gini coefficients for cumulative volume, which is equivalent to the growth dominance coefficient (GDC)

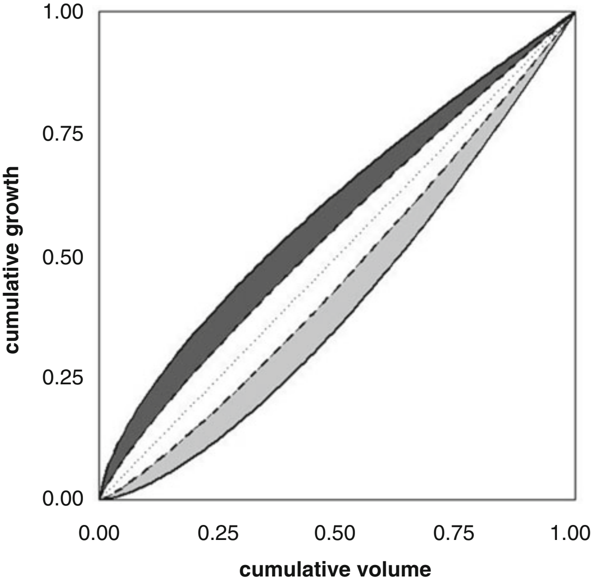


Fig. 2.7 Representation of the cumulative distribution of tree volume growth over cumulative tree volume for pure (solid lines) and mixed stands (dashed lines). Dark grey for dominance of small trees and light grey for dominance of large trees

used by Binkley et al. (2006). This coefficient is zero (GDC = 0) when all trees contribute to stand growth proportionally to their volume, GDC > 0 when there is a growth dominance of tall trees, and GDC < 0 when there is a growth dominance of small trees. Katholnig (2012) found that in the average even-aged and uneven-aged mixed-species stands, the GDC was negative, while it was positive for pure stands. However, Pretzsch et al. (2016) reported no differences in GDC between pure and mixed stands of Scots pine and European beech.

The mode of competition can be directly analysed through the direct exploration of growth-size relationships (Weiner 1990; Pretzsch and Biber 2010), which can also be employed to compare the mode of competition in mixed versus in pure stands (Pretzsch and Schütze 2014, 2015).

2.5.3 Age Structure

When characterizing the structure of a mixed stand, age structure (aggregation of stand-level ages) should also be taken into account as it is related to productivity, sustainability, biodiversity or carbon dynamics (e.g. Forrester and Bauhus 2016; Thurm and Pretzsch 2016; Musavi et al. 2017). The age structure is frequently summarized in a single indicator, which implies the use of different definitions according to the requirements of each study (e.g. Garet et al. 2012 analysed the use of dominant age as an indicator of sustainability by measuring four to nine randomly selected dominant or codominant trees, avoiding overdominant or overstorey trees). As for monospecific stands, the terms even-aged, two-aged and uneven-aged are used to refer to the age composition.

Assigning an age to an even-aged mixed forest is not technically problematic and can be determined by coring individual trees. However, the number of cored trees per species used to estimate stand age can vary greatly among studies (Chen et al. 2003; Lei et al. 2009; Waskiewicz et al. 2013). In uneven-aged stands, stand age is often replaced by the dominant age (Garet et al. 2012) or dominant age by species (Lee et al. 2004) as it is possible to characterize the stand from a small sample of cored trees. Despite its usefulness for stand characterization, the mean age of dominant trees by species provides little data as regards the real age structure of the mixed stand (Lee et al. 2004).

Due to the difficulties associated with age determination, diameter or other size indices are often used as a surrogate for age. The most common index is the number of large trees, sometimes referred to as number of old-growth trees (Barbati et al. 2012), by using a threshold diameter to define large trees ranging from dbh >65 cm to dbh >100 cm (Mc Elhinny et al. 2005) or specifying a threshold by species (Alberdi et al. 2013). The use of the mean diameter of larger trees does not require tree core sampling, although as it is a surrogate for age, it does not allow real age to be assessed (Ziegler 2000). Despite the difficulty and expense involved in age structure estimation of mixed stands, it is important to consider this stand characteristic as it is related to stand productivity (showing different patterns in mixed forest for a variety of age structures; e.g. Binkley and Greene 1983; Waskiewicz et al. 2013) and to forest dynamics (e.g. Coomes and Allen 2007).

2.6 Stand Productivity

Productivity is a key stand characteristic for forest management as it is an important indicator of forest functions and services. Stand productivity is directly linked to site conditions, although it is also influenced by stand structure, including species composition. Many studies have found that mixing forest tree species may result in over- or underyielding (Pretzsch 2018) when compared to the productivity in corresponding monospecific stands. There has long been interest in forest practice and science in estimating site productivity through site indices, which provide a well-developed tool for even-aged monospecific stands (Skovsgaard and Vanclay 2008). In this section we review stand productivity indices and their applicability in mixed stands and present methods for comparing stand productivity in mixed versus monospecific stands.

2.6.1 Stand Site Productivity Indices

Site indices are based on three fundamentals (Skovsgaard and Vanclay 2008): site classification by stand height, Eichhorn's rule and the thinning response hypothesis. What follows is a brief review of the ways the first fundamental component has been applied in mixed forests. Site index (SI) is the dominant height of a stand at a reference age. It is an indicator of site productivity and has little value unless it is accompanied by a volume production indication (Eichhorn's rule). In management or in forest growth models of pure, even-aged stands, it is used to classify stands according to their timber productivity (Burkhart and Tomé 2012 and references therein).

However, its applicability to mixed forests is dubious because dominant height growth might be affected by competition with the other species, especially in the case of slower-growing species. The more deviation from an even-aged, monospecific situation, the greater the competition confounding effects on the height-age relationship (Pretzsch 2009). This means that species-specific height growth response would indicate competitive conditions instead of site features (Pretzsch and Zenner 2017) leading to misleading height-age relationships. Accordingly, Vallet and Perot (2016) reported significant, although weak, mixing effects on dominant height. Even though dominant heights of mixed stands cannot be used to estimate site index due to the lack of site index models for mixed stands, another problem is the approach used to estimate dominant heights for mixed stands. One approach is to not consider tree species identities when selecting dominant trees (Zingg 1994). The other option would be to calculate dominant heights by species considering the area occupied by each species (Keller 1995). However, for a given site and age, these dominant heights will depend on species proportion (Sterba 1996).

Although the dependency of site index on height and age makes its use in uneven-aged and mixed stands somewhat problematic, the concept is so deeply rooted in our understanding of forest growth that it is often adapted to mixed forests. Some examples are (1) the site index conversion equations where the SI of one species is estimated from the SI of a second species growing in a mixed stand (Vospernik and Sterba 2001; Nigh 2002), (2) the SI of the dominant species (Edgar and Burk 2001; Hein and Dhote 2006), (3) the same SI equation for conspecific species (Eriksson et al. 1997), (4) the SI for each of the component species (Bollandsas et al. 2008) or (5) the SI of one dominant species using parameter estimates of a full model fitted to all species in the mixture (Waskiewicz et al. 2013).

Alternatively, SI has been substituted in forest growth models of mixed or uneven-aged stands by means of a past growth index (Trasobares et al. 2004b; Palahí et al. 2008), actual site variables (Trasobares et al. 2004a) or applying an age-independent site index approach (Tomé et al. 2006). The specific height attained at a reference diameter based on the allometric height-diameter relation has also been proposed as a productivity index in southern uneven-aged and boreal mixed forests (Vanclay and Henry 1988; Huang and Titus 1993). Vanclay (1992) proposed a growth index for complex mixed tropical forests based on the diameter increment adjusted for tree size (diameter) and competition (BAL). He also suggested that periodic annual volume increment might indicate site productivity, especially in cases where no management is carried out (i.e. thinning or release of trees). Other studies have avoided the use of site index in mixed forests by including site environmental variables in models (Monserud and Sterba 1996; Vallet and Perot

2011; Adame et al. 2014; Toïgo et al. 2015). This method is promising as a way to account for site productivity, as environmental variables at larger scales are becoming increasingly available.

2.6.2 *Comparison of Productivity in Mixed Versus Monospecific Stands*

Over- or underyielding in mixed stands in comparison to monospecific stands may be due to interactions between species (Toïgo et al. 2015). These interactions are frequently described as competition, facilitation and competitive reduction (Forrester and Bauhus 2016; Pretzsch et al. 2013). Because the individual contributions of these three mechanisms are difficult to isolate, they are frequently described collectively as complementarity (Loreau and Hector 2001; Mina et al. 2017).

For a variety of reasons, foresters may not only be interested in how total growth of all species as a whole in a mixed stand compares to growth in monospecific stands (e.g. different commercial value of the species) but may also be interested in the behaviour of individual species in the mixture compared with their growth in the respective monospecific stands. For these species-wise growth comparisons, the correct definition of the species proportions is crucial. If the growth per area is to be compared, the area attributed to the species in the mixed stand has to be defined by relating the observed density of the species to its maximum density (Dirnberger and Sterba 2014; Huber et al. 2014; Sterba et al. 2014; Dirnberger et al. 2017).

The different species in mixed stands may show differences in growth habit, specific wood gravity and species-specific growth rates that may impede the use of volume as a direct measure of site productivity (Vanclay 1994). As a consequence, total biomass or biomass growth would appear to be a better alternative when comparing the production of mixed versus pure stands (Pretzsch et al. 2013). However, due to the lack of species-specific knowledge along with the fact that timber is usually sold by volume, using total volume or volume growth is the most frequently employed option.

In order to determine whether mixing affects productivity for a given species i, the observed productivity (i.e. growth, total volume or biomass) of this species in a mixed stand ($P_{i,\mathrm{mix}}$) is compared to the reference productivity of the species ($P_{i,\mathrm{ref}}$), assuming the hypothesis that there is no mixing effect ($P_{i,\mathrm{ref}} = P_i \cdot m_i$), i.e. the productivity of the species is equal to its productivity in a monospecific stand (P_i) times its proportion in the mixed stand (m_i) (Table 2.5). The observed productivity for the total mixed stand ($P_{\mathrm{mix}} = \Sigma pp_{i,\mathrm{mix}}$) can be compared to the sum of the reference productivities of all the species in the mixture ($P_{\mathrm{ref}} = \Sigma P_i \cdot m_i$). If the observed productivity is higher than the reference productivity ($P_{\mathrm{mix}} > P_{\mathrm{ref}}$), this evidences a positive mixing effect (overyielding), whereas the opposite is true (underyielding) if the observed productivity is lower ($P_{\mathrm{mix}} < P_{\mathrm{ref}}$). It is particularly interesting when there is transgressive overyielding, i.e. the productivity of the mixed stand exceeds the productivity of the best growing respective pure stands

Table 2.5 Measures for comparing productivity in mixed versus monospecific stands. To simplify the presentation, the measures are given for mixed stands composed of only two species, following the nomenclature used by Pretzsch et al. (2013)

	Species 1	Species 2	Total
Basic productivity variables			
Monospecific stand	P_1	P_2	–
Mixed stand	$pp_{1,(2)}$	$pp_{(1),2}$	$P_{1,2} = pp_{1,(2)} + pp_{(1),2}$
Mixed stand upscaled to hectare	$P_{1,(2)} = pp_{1,(2)}/m_1$	$P_{(1),2} = pp_{(1),2}/m_2$	–
Mixed stand reference	$P_1 \cdot m_1$	$P_2 \cdot m_2$	$\widehat{P}_{1,2} = P_1 \cdot m_1 + P_2 \cdot m_2$
Comparison measures			
Absolute over-/underyielding	$P_{1,(2)} - P_1$	$P_{(1),2} - P_2$	$P_{1,2} - \widehat{P}_{1,2}$
Relative productivity (mixed/monospecific)	$\mathrm{RP}_{1,(2)} = P_{1,(2)}/P_1$	$\mathrm{RP}_{(1),2} = P_{(1),2}/P_2$	$\mathrm{RP}_{\mathrm{mix}} = \mathrm{RP}_{1,2} = P_{1,2}/\widehat{P}_{1,2}$
Ratio of productivity based on relative productivity	$\mathrm{RPP}_{1,(2)} = pp_{1,(2)}/P_1$	$\mathrm{RPP}_{(1),2} = pp_{(1),2}/P_2$	$\mathrm{RPP}_{1,2} = \mathrm{RPP}_{1,(2)} + \mathrm{RPP}_{(1),2}$
Relative over-/underyielding	$m_1/\mathrm{RPP}_{1,(2)}-1$	$m_2/\mathrm{RPP}_{(1),2}-1$	$\mathrm{RPP}_{1,2}-1$

($P_{\mathrm{mix}} > \max\{P_1, \ldots, P_i, \ldots P_n\}$). Analogously, degressive underyielding occurs when the productivity in mixed stands is lower than the respective productivity in the worst growing pure stands ($P_{\mathrm{mix}} < \min\{P_1, \ldots, P_i, \ldots P_n\}$). Extending the term "over-/underyielding" to the individual species, overyielding is when the observed productivity of the species in the mixed stand is greater than the respective reference productivity ($P_{i,\mathrm{mix}} > P_{i,\mathrm{ref}}$), provided that $\mathrm{m_i}$ is the correct species proportion by area. The graphical representation of these relationships for a two-species mixture is known as Kelty's (1992) replacement series or cross-species diagrams (Harper 1977; Fig. 2.8).

The comparison between productivity in mixed versus monospecific stands can also be expressed in relative terms (ratio mixed vs. monospecific) by species as well as for the total stand (Pretzsch et al. 2010, 2013; Bielak et al. 2014, 2015), i.e. the relative productivity by species (RP_i) and the relative productivity for the total stand ($\mathrm{RP}_{\mathrm{mix}}$: Table 2.5), also called ratio of productivity based on absolute productivity (Pretzsch and Forrester, 2017). Similarly, the ratio of productivity based on relative productivity (RPP) can be used to compare productivity in mixed versus monospecific stands (Harper 1977). The RPP (Table 2.5) gives the observed productivity (total yield or growth) in the mixed stand in relation to the productivity of the monospecific stands ($\mathrm{RPP}=\Sigma pp_{i,\mathrm{mix}}/P_i$). The ratio $pp_{i,\mathrm{mix}}/P_i$ quantifies the required land area of pure stand to produce the same yield for species i and does not explicitly use species proportions. If, however, this required land area is larger than its estimated proportion m_i, the species is overyielding, because it needs less area in the mixed stand to produce the same growth as in the monospecific stand. The RPP is equal to the relative yield total and land equivalent ratio which are common in herbaceous plant biology and agronomy (Vandermeer 1989, pp. 19–20). Note that the relative productivity $\mathrm{RP}_{1,2}$ is expressed in terms of productivity, while the "ratio

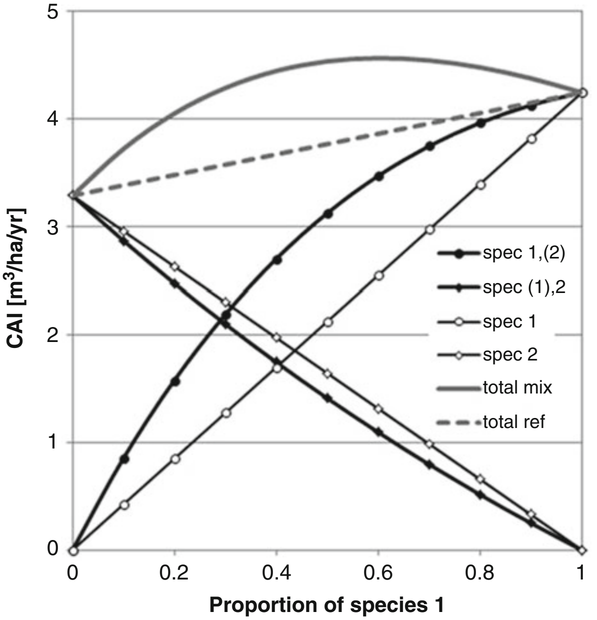


Fig. 2.8 Schematic representation of mixing effects by cross diagrams according to Harper (1977). In this example, species 1 has a higher current annual increment (CAI) in the pure stands (species proportion = 1) than species 2 (CAI when proportion of species 1 is 0). In the mixed stand, species 1 exhibits a positive mixing effect (sp1,(2)), i.e. it shows better growth than its reference. Species 2 exhibits a minor negative mixing effect (sp(1),2). Both species together present a positive mixing effect, not only displaying higher increment than the reference but also exhibiting transgressive overyielding, as the increment is greater than that of a pure stand of the species with the best growth, where the species proportion of species 1 is between 0.25 and 1

of productivity" $RPP_{1,2}$ is expressed in terms of area and therefore different. Similar methods of weighting by species proportion can be used to compare other stand variables in mixed versus monospecific stands (Forrester and Pretzsch 2015). For such comparisons, the proportion of the species in the mixed stand (m_i) must be the fraction of the stand area available for the respective species.

2.7 Concluding Remarks

Characterization of complex forest stands requires the use of measures and indices which properly reflects all the components of stand structure and productivity. Although there are a large number of existing measures and indicators as presented in this review, there are still certain challenges which require further attention. Firstly, there are some methodological aspects related to measures or index definitions which are not entirely clear for certain attributes such as stand density or site productivity. Secondly, the implications of using different indices for a given attribute when analysing mixed stands are relatively unknown. Finally, the effects of certain stand structure components on forest dynamics and productivity have scarcely been addressed.

One challenging area concerns maximum stand density and self-thinning in mixed forests. When using maximum stand densities in monospecific stands of component species as a reference to estimate stand density and species proportion in mixed stands, it is critical to consider species-specific MSDRs and their variability with site conditions (Condés et al. 2017; Aguirre et al. 2018) as these can cause variation in competition equivalence coefficients and species proportions (Fig. 2.1), with corresponding effects on the assessment of stand dynamics and productivity (Sterba et al. 2014). In any case, species interactions can result in over-density in comparison to monospecific stands (Pretzsch and Biber 2016; Pretzsch 2018); therefore size-density trajectories and their dependence on species composition must be understood for different mixtures. This is important for the estimation of density and yield level, for the development of silvicultural guidelines such as stand density diagrams (SDMD) and for forest modelling. Theoretically, a stand density index based on the MSDR defined in such a way that it integrates the stand density in pure stands as specific cases of mixed stands, as well as variation with site conditions, would be the best option. Hence, approaches such as those used by Ducey et al. (2017) and Bravo-Oviedo et al. (2018) seem promising.

As regards site productivity, finding a comprehensive indicator for mixed stands continues to be a challenge, although three basic properties have been identified: (1) the indicator must be age independent, (2) it should be a good descriptor of the site properties, and (3) it should be correlated with total biomass production and represent all the mixture effects along environmental gradients. The fact that for certain mixtures, over-/underyielding varies with productivity gradients, taking pure stand productivity as a reference (Forrester et al. 2013; Pretzsch et al. 2010, 2013; Toïgo et al. 2015), underlines the need for a specific productivity indicator for mixed forests.

Accordingly, changes in net species interactions along abiotic gradients need further exploration, considering the effect of using different methods to represent gradients. In mixed stands, species have different ecological traits and limitations, so the site conditions need to be specifically quantified in terms of the prevailing resources (light, water, mineral nutrients) and other environmental factors (temperature, length of the growing season, etc.). The most limiting factors are generally better known in the case of pure stands, and therefore these factors can be used to define the abiotic gradient for the analysis of mixed stands (Toïgo et al. 2015). However, this approach is complicated by the fact that it is not always easy to identify the environmental factors which have the greatest influence on complementarity (Forrester 2014). In a number of studies, site index in pure stands has been used as a surrogate of abiotic gradients under the assumption that productivity is linked to abiotic gradients (Pretzsch et al. 2010, 2013, 2015). However, for certain species compositions, different patterns were found for the different species in the mixture, therefore making it difficult to interpret and generalize the results for the whole stand.

Different approaches can be used to estimate species proportions, and the best approach to use may depend on the objective pursued. Thus, the proportion of the species by tree number may be important when analysing the survival and fitness of the species cohort; the species' share of the stand surface area may be best when the focus is resource acquisition and growth, while the number of functional groups may be of interest when evaluating resistance and resilience. Studies which have compared different approaches to estimate species proportions using the same data (Pretzsch 2009, pp. 359–360; Huber et al. 2014; Dirnberger and Sterba 2014; Dirnberger et al. 2017) have clearly demonstrated that different approaches result in different proportions, which in turn leads to differences in the subsequent analysis. A general conclusion can be drawn that species proportion is not a variable that can be estimated without errors. Consequently, appropriate statistical methods should be used which account for these errors if species proportion is used as an independent variable. Differences in growth dynamics, not only between species but also within the same species for mixed and pure stands (Pretzsch 2005), lead to changes in species proportions over time. Hence, care must be taken when analysing long-term data (Puettmann et al. 1992).

The different stand structure characteristics may have a strong influence on mixing reactions. However, most previous studies addressing mixing effects have focused mainly on stand density and species composition. Although tree distribution pattern and size distribution indices have been used to describe mixed stands, their influence on mixing reactions needs to be understood with greater clarity. Not including these characteristics in the analysis could lead to misinterpretations of the mixing effects (Leikola 1999; Schütz 1999). Furthermore, the stand structure measures introduced in this chapter should be analysed at both stand and species level. While the analyses at the stand level address the practical consequences of species mixing, analyses at species level contribute towards a better understanding of the effects found at stand level. Therefore, the effects on the results at stand level of many of the measures and methods presented here must be carefully scrutinized. If the methods for quantifying and evaluating stand structure, dynamics and productivity in mixed forests are not standardized and tested in terms of their influence on mixing reactions, the strength of any evidence as regards mixing effects remains low.

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Chapter 3
Data Platforms for Mixed Forest Research: Contributions from the EuMIXFOR Network

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Abstract Forest inventory data, observational studies (mensurative and manipulative), and planted experiments provide the main data sources for the study of mixed forests. Demonstrative experiments such as marteloscopes are also basic to both research and training. Under the umbrella of the EuMIXFOR project, several research efforts have been conducted to further our knowledge as regards the functioning and development of mixed forests. Within this project, information from different forest research experiments at European level focusing on mixed forests has been compiled in order to identify the current state of the art. In the case of the European beech and Scots pine mixture, a gradient of triplets of monospecific and pure plots of these species has been established across Europe. Common establishment and measurement protocols have been developed in order to

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harmonize comparisons and analyses. Data sharing is also an objective; therefore, data from the triplet study of the European beech and Scots pine mixture are now available. A common dataset with the National Forest Inventory data from some European countries has been used for the study of mixtures.

3.1 Introduction

Professionals from different fields including scientists, forest practitioners, and forest policy makers all have an interest in furthering our knowledge as regards the effects of species mixtures on forest functioning and development. It is commonly assumed that tree species diversity has positive effects on ecosystem functioning, e.g., forest productivity (Zhang et al. 2012; Liang et al. 2016). Various factors affect these relationships, such as climatic conditions, substrate, resource availability, successional stage, mixing proportion, or stand density (Forrester and Bauhus 2016). However, few studies have investigated different ecosystem functions simultaneously in order to confirm that tree diversity enhances forest multifunctionality as a result of trade-offs and synergies between functions (Gamfeldt et al. 2013). When analyzing the effects of species admixture on ecosystem services, monospecific stands of the species which comprise the mixture can serve as a reference. Empirical data from long-term or temporal research plots, forest inventories, and mixed plantation experiments provide an appropriate data source. Thus, the effects on soil characteristics, water supply, pests and pathogens, growth and yield, or carbon sequestration can be evaluated.

Forest management and disturbances can modify species composition and/or mixing proportions, which in turn affect the relationships with ecosystem function. Specific experimental designs, e.g., trials with varying thinning intensities, regeneration felling, or fertilization, provide insights into the effects of forest management and disturbances (Mason et al. 2018; Pach et al. 2018).

In recent decades, experiments involving planting of mixed forest have been established enabling forest dynamics at young ages to be observed. Such experiments are essential as planted forest area has been increasing at a mean rate of 4.2 million ha per year over the last 25 years and currently account for 8% of the

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global forest area (FAO 2016). Although most plantations are monocultures, there are many benefits associated with mixed forest plantations, and interest in this type of plantation is currently increasing, with the aim of providing a broader range of ecosystem services (Paquette and Messier 2010; Urgoiti and Paquette 2018).

Over the last few decades, demonstrative experiments such as marteloscopes (Soucy et al. 2016) have gained prominence, in particular when established in mixed forests. They offer a valuable approach for training and for testing different silvicultural treatments. Together with forest growth models applicable to mixed forests (Fabrika et al. 2018), marteloscopes allow future stand development and the effects of management strategies to be identified as well as quantified.

In this chapter, we firstly describe the main characteristics of the different data sources for studying mixing effects on forests, and secondly, we describe our experience in developing and using data platforms under the umbrella of the EuMIXFOR European project.

3.2 Data Sources

3.2.1 Forest Inventories

National or regional forest inventories are commonly based on a statistical sampling design, e.g., permanently and systematically distributed inventory plots within a given landscape, where plots have to be remeasured, usually every 5–10 years, to determine the increment or the variation in the different attributes. In the past, the main objective of the National Forest Inventories (NFIs) was to present an assessment of wood resources at landscape level, although today the scope of these inventories is wider (Tomppo et al. 2010a). NFIs have been extended to include information related to ecosystem functions, e.g., recording variables for biodiversity, attributes of forest health, non-wood forest products, etc. (Corona et al. 2011; Alberdi et al. 2014; Hernández et al. 2016). Moreover, much effort has been invested in attempting to harmonize the definitions used in forest inventories in Europe, thus allowing comparison between estimations (Tomppo et al. 2010b).

The main advantage of using data from NFI or regional forest inventories is that various forest types across a broad range of environmental conditions are represented. These data, together with auxiliary data, e.g., site information, can be used to explore the effects of tree species admixture in relation to forest productivity. Additionally, such data can contribute to the development of silvicultural guidelines for mixed forest management (Condés et al. 2017).

There are also certain limitations associated with the use of forest inventory data to study mixed forests. For example, tree species diversity can be masked by environmental variables, although only a few of these are usually recorded (Vilà et al. 2005; Baeten et al. 2013). Other challenges include the estimation of growth and yield of rare species, since these may only account for a very small proportion within the stands (Bauhus et al. 2017). Furthermore, as large parts of forest stands are managed, such management reduces stocking density and controls species composition, for example, by promoting the most productive species in terms of timber. Hence, it can be difficult to determine the effects of mixing if the stand density is below the maximum density at which mixing effects are most evident. Indeed, the influence of mixing effects may have disappeared (Bauhus et al. 2017). Nevertheless, several studies have addressed the possible influence of density on mixing effects (Condés et al. 2013; Huber et al. 2014).

There are several examples in the literature where forest inventory data is used to test hypotheses concerning the possible benefits of mixed forests. These studies can be divided into those testing the effects of tree species diversity or tree species richness on forest functioning and those which focus on specific mixtures (largely two-species mixtures). As examples of the former, Vilà et al. (2007), using data from the Spanish National Forest Inventory, found higher wood production in mixed forests in the NW of Spain in comparison with monospecific stands. Paquette and Messier (2011), using data from the Québec (Canada) forest survey, found a significant, positive effect of biodiversity on tree productivity. A general positive relationship was also found between species richness and wood production, for example, by Ruiz-Benito et al. (2014) for Spanish forests and by Vilà et al. (2013) using data from five European countries. Gamfeldt et al. (2013) considered other variables in addition to productivity, such as berry production, soil carbon storage, understory plant species richness, and deadwood. These authors reported that stands in which five species were present showed greater ecosystem services, including biomass production, than those with only one species.

However, despite these general results, no patterns can be identified for specific mixtures: the effects of competition as well as the influence of the environment being species-specific. Several studies using NFI data have identified through tree-level or stand-level models that the positive or negative complementarity between the species in a mixture depends on both the specific composition (Hein and Dhote 2006; del Río et al. 2014) and the environmental conditions such as climate, soil conditions, or even stand density or structure (Condés et al. 2013; Huber et al. 2014; Condés and del Río 2015; Mina et al. 2018). For example, del Río and Sterba (2009), using the Spanish National Forest Inventory data, found that productivity was higher in mixtures of *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. than in monocultures; Vallet and Pérot (2011), basing their study on data from the French National Forest Inventory, reported that silver fir and Norway spruce (*Picea abies* (L.) Karst.) mixtures had higher productivity. Toïgo et al. (2015), using French National Inventory data, found that overyielding was greater in low productivity sites for a number of two-species mixtures. Furthermore, Toïgo et al. (2017), again using French Forest Inventory data, determined that overyielding in *Quercus petraea* (Matt.) Liebl. mixtures was related to shade tolerance in the companion species.

3.2.2 Observational Studies (Exploratory)

Data recorded in observational plots are generally more exhaustive than forest inventories. These kinds of trials are commonly established in mature forests along tree diversity gradients while maximally controlling other environmental variables (Baeten et al. 2013). However, other aspects may not be controlled, such as past stand conditions (silviculture and age structure) or the variability of soil or climatic conditions, even for the same site (Forrester and Pretzsch 2015). According to Hurlbert (1984), observational experiments can be mensurative experiments or manipulative experiments.

Observational experiments present the advantage of being carried out in mature forests, where the tree size distribution, structure, and species composition can be more representative of actual forests in comparison to plantation experiments. Moreover, if the trials are reproduced at several sites and for different ages, the conclusions drawn will be more universal (Bauhus et al. 2017).

- *Mensurative experiments* only involve measurements at one or more points in space or time, with no external factors considered as treatments. There are several datasets from long-term observational plots in different countries that provide a valuable tool to analyze relationships between forest diversity and ecosystem functioning, although plot selection was not based on a diversity criterion (Scherer-Lorenzen 2014). In accordance with Zhao et al. (2014), data from mensurative experiments can be divided into longitudinal, cross-sectional, and interval studies. In long-term mensurative experiments (longitudinal studies), the same individuals are measured recurrently over time. Hence, a length of time is required to obtain results. Cross-sectional experiments or chronosequences involve single measurements of experimental plots, differing only in age. However, guaranteeing similar growing conditions for all plots involved can be problematic. Interval studies are a compromise between the two above approaches in which the rate of change of a variable of interest is measured at least twice over a time range.

  Examples of the effect of species interactions in two-species mixture forests using long-term datasets from mensurative experiments can be found in the literature. For example, Pretzsch and Schütze (2009) found that mixtures of Norway spruce and European beech (*Fagus sylvatica* L.) produce more aboveground biomass than pure stands; Forrester et al. (2013) reported that complementarity between silver fir (*Abies alba* Mill.) and Norway spruce was dependent on climate, site quality, and stand density; Bielak et al. (2014) stated that mixtures of Scots pine (*Pinus sylvestris* L.) and Norway spruce were more productive than pure stands; and Pretzsch et al. (2015) found a higher productivity in mixtures of Scots pine and European beech. However, there are also large-scale experiments that have been established along tree diversity gradients in mature forests (Baeten et al. 2013), such as those included in the FunDivEUROPE platform (www.fundiveurope.eu). Grossiord et al. (2014) reported that higher diversity only enhances resistance to drought in drought-prone environments; Jucker et al.

(2014) stated that the effects of diversity on productivity become stronger in stressful environments and reported a greater temporal stability of growth rates in mixed forests; Guyot et al. (2016) found a positive relationship between tree species richness and resistance to insect herbivores; and Dawud et al. (2017) reported a small positive influence of tree species diversity on soil carbon stocks, the functional group having an important effect.

- *Manipulative experiments* consist of two or more treatments that are randomly applied to experimental units to determine their effects. Thinning or silvicultural experiments in general or fertilizing trials fall into this category. Although this kind of trial provides a lot of information on growth, yield, and effects of silviculture, it also presents certain disadvantages, such as the high cost of maintaining the field experiments and the restricted ability to generalize beyond the homogeneous and limited experimental conditions (Zhao et al. 2014). Less information and results are available from manipulative experiments in mixed forests than from monocultures, although some can be found in the literature. For example, results obtained by some authors as Pretzsch (2003) concerning the superior growth of Norway spruce and European beech in mixed vs. pure stands over a range of densities; Cotillas et al. (2009) studied thinning and rainfall reduction in mixed oak coppices; Primicia et al. (2016) described the use of moderate thinning in the early stages of mixed Scots pine and European beech forests in the Pyrenees (Spain); and Aldea et al. (2017) found a higher radial increment response to drought in heavily thinned Mediterranean oak (*Quercus pyrenaica* Willd.) and maritime pine (*Pinus pinaster* Ait.) stands.

3.2.3 Mixed-Species Plantation Experiments

Planted experimental sites are necessary in order to further our knowledge on the development of mixed-species plantations, the diversity, and the effects on species identity, species proportions in plantations, etc.

Experiments in which the diversity effects are separated from species identity have been established with greater frequency since the end of last century in the form of mixed-species plantations and are termed "tree diversity experiments." However, plant density and species proportion trials have been conducted since the middle of the twentieth century in order to increase our understanding of plant development during the very early stages.

3.2.3.1 Tree Diversity Experiments

The purpose of these trials is to detect and quantify relationships between species diversity and ecosystem functioning, known as biodiversity-ecosystem functioning. Most of the tree diversity experiments established during last 20 years are now included in the global network TreedDivNet (www.treedivnet.ugent.be). Plantations of tree communities with different degrees of tree diversity have been created, with gradients of tree species richness, genetic diversity, number of functional groups, or continuous gradients of functional diversity (Scherer-Lorenzen 2014). The most important characteristic of these experiments is that tree species are grown in both monocultures and mixtures and that diversity levels are replicated in a randomized design (Verheyen et al. 2016).

3.2.3.2 Plant Density and Species Proportion Experiments

Determining appropriate plant density and species proportions in the establishment of mixed forest plantations is very important. Common designs for studying plant density and species proportions are the substitutive or the additive design plantations (Kelty and Cameron 1995; Scherer-Lorenzen et al. 2005).

The substitutive design (also known as "replacement series") requires the initial plant density to be kept constant across all plots of the experiment, and different species proportions are tested among plots (Kelty and Cameron 1995). In the case of two-species studies, the proportion tested can be 100:0, 75:25, 66:34, 50:50, 34:66, 25:75, and 0:100 of the plantation density (or other proportions depending on the objectives of the experiment). Monocultures of the two species (100:0 and 0:100) are required in order to identify the behavior of the species with only intraspecific competition. Tree-by-tree or row-by-row mixing patterns can maximize interactions between species since every tree has at least two competitors of the other species. In order to determine the effect of the plant density, different density series using this design can be established to allow the separation of mixing and density effects (Kelty and Cameron 1995; Bauhus et al. 2017). This kind of design has been widely used in forestry. Among others, replacement series were included in studies by Amoroso and Turnblom (2006) in the Northwest USA, Forrester and Smith (2012) in Australia, or Nunes et al. (2014) in Portugal. In many cases, these plant density designs commonly included N-fixing species in order to increase productivity and maintain soil fertility (e.g., Binkley et al. 2003; Forrester et al. 2004). The information provided by substitutive series is particularly valuable during the first stages of stand development. At later stages, the increase in tree size, with differing growth rates of the species and increasing competition conditions, will lead to changes in plant density and species proportions if natural mortality processes appear.

Under the additive design, the stocking density in mixed plots is the sum of the density of the monoculture plots, since all the species are added in the mixture. Generally, one species density is constant and the other is added at different densities. There are only a few examples of additive design in forestry. For example, Bell et al. (2000) used this design to study the competitiveness of different species with jack pine and black spruce seedlings in Canada. Bouillet et al. (2013) also used this design to study tree growth in *Eucalyptus* and *Acacia* mixed plantations in Brazil and Congo.

Kelty (2006) highlighted the need for other research approaches to further our understanding of development and production in mixed plantations. Species trials, continued research into species interactions and operational trials are needed.

Specific plantation designs can be used to analyze the competition between plants at tree level. Such designs can be used to test spacing in mixed plantations using distance-dependent models (Kelty and Cameron 1995). According to these authors, the growth of individual trees depends on the number, size, and species of the neighboring trees and on the distances between them. In these distance-dependent designs, a "regular grid" can be used in which each tree is equally spaced from its neighbors. In a Nelder wheel design, the trees are planted in a circular plot in concentric rings radiating outward with spokes connecting the center with the furthest ring (Parrott et al. 2011). A tree is planted at each intersection between spokes and arcs, creating variable tree densities within the plot. This reduces the need for an additional experimental plot for each density, although stand-level information is not obtained. In the analysis, each tree is assigned to a fixed space, determined using a Voronoi polygon, and if tree mortality occurs, the space allocated to each tree is modified accordingly (Ruano et al. in preparation; Ruano and Bravo, in preparation). Another specific design for testing tree species in plantations is the Goelz design (Goelz 2001; Vanclay 2006). This involves a triangular plot in which the species composition varies gradually from each corner to the opposite face and the species proportion is determined by the location in the triangular plot.

3.2.4 Demonstrative Experiments: The Use of Marteloscopes as Training and Communication Platforms for Silviculture in Mixed Forests

Forest management is rapidly evolving as novel approaches arise (e.g., Nagel et al. 2017; Nocentini et al. 2017) and new techniques and tools become available (e.g., Corona 2016). However, implementation within operative processes should be evidence-based (Corona 2014), i.e., based on objective, reliable assessment. In this context, silvicultural approaches and management tools should be properly tested prior to being passed on to stakeholders. Adequate supporting infrastructures such as marteloscopes, which are specifically conceived for testing, training, and teaching of silvicultural approaches, provide a strategic tool for this purpose (Soucy et al. 2016). Marteloscopes can be particularly suitable for testing the effect of management when forest composition is modified by stocking reduction in mixed forests.

Marteloscopes (from the French term *martelage* = marking trees for cutting) have been used for decades in many European countries for silvicultural training. A marteloscope is a forest stand in which all trees are numbered and mapped; the species are identified and measured for tree marking simulations (Fig. 3.1). In combination with a software tool, forest professionals, workers, researchers, and

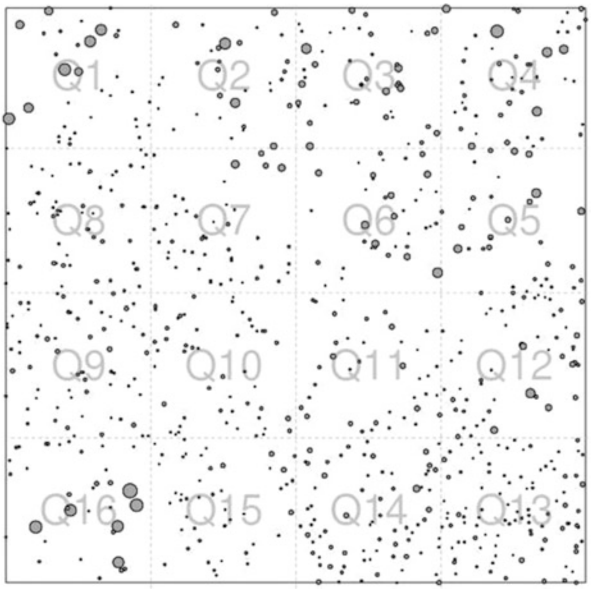

Fig. 3.1 Example of a marteloscope (Abetone, Italy, about 1.5 ha wide). Dot size is proportional to tree stem diameter

students can mark trees for removal, based on specified approaches and/or management goals, and can directly assess the outcome of their marking in these areas.

Homogeneous stands (monocultures; even-aged stands) are generally suitable for teaching and training in classical and extensive silvicultural treatments, while heterogeneous stands (mixed; uneven-aged stands) are more useful for testing innovative treatments. A network of both types of marteloscope (established in homogenous and heterogeneous stands) may be suitable to test approaches for different stand structures and forest types across a given country or region.

Marteloscopes are characterized by complete data for every tree. Besides tree species recognition, diameter at breast height and height are recorded, and derived attributes such as basal area, volume, or biomass are also calculated. Additional data may be recorded, for example, the rank of each tree according to social position (e.g., dominant, intermediate, dominated tree), the crown projection on the ground (to derive crown area), the crown shape (i.e., crown depth, height of maximum width), or the stem quality. The more data are provided, the more comprehensively the simulated interventions can be evaluated. Although forest professionals and technicians are usually interested primarily in wood harvesting (with tree volumes as mandatory data), many other aspects (e.g., canopy gap or wildlife habitat analysis) can be derived from additional data recorded for each tree.

Interactive platforms (Fig. 3.2) are used to summarize and analyze the effects of the simulated silvicultural interventions, showing current conditions and the immediate outcomes of the virtual tree selection (removals and residuals). If appropriate growth models are available and implemented for the species growing in the mixtures, the effects on growth and on stand structure can also be determined. 3D

Integrate+ software

Integrate+ uses a well designed software tool which runs on mobile devices (tablets). Those can be used directly on the Marteloscope sites in the forest.

In advance of virtual tree selection or other exercises the software facilitates pre-settings for the training in the field. Also, it offers and displays a detailed description of individual tree microhabitats and their relevance for different biomes and species.

During or after performing the training exercises, users receive direct feedback on all silvicultural decisions they have implemented on site both in qualitative and quantitative figures. These outputs serve for self- or group evaluation, comparison of results and education.

An important aim of the software is that user groups can discuss on the basis of objecti concepts and practical approaches on site. This way, participants can benefit from exchang decision making capacities.

There are three software packages available and tailored for different user groups:

I+ Trainer

This software package is applied when running exercises on the Marteloscope sites. It is typ

- selecting specific M-Scope area and type of exercise (possibly automated)
- performing exercises
- computing and displaying initial results
- revising of initial selections and rerun exercises
- presenting and storing final exercise results

I+ Manager

The I+ Manager software package allows the core users to:

- enter new Marteloscopes datasets
- maintain existing Marteloscope information
- introduce new variables that are agreed upon and are added to all Marteloscopes
- defining Marteloscope exercises
- synchronize the local databases on the tablet computers (see section on I+ database)

I+ Database

There are two major datasets which are co-located in one master database. One set contains all variables that have been assessed in a Marteloscope, while the second comprises of the data that is needed to conduct the tailored training sessions.

The database is located on each mobile device (tablet computer). When the tablet is connected to the Internet, it will synchronize its 'local' database with that of the main server database and update with any new information. Also, training session results from the tablet are uploaded to the master database on the server.

Fig. 3.2 The Integrate+ software, available at http://www.integrateplus.org/integrate-software.html, and the Smartelo software, available at http://sostenible.palencia.uva.es/content/smartelo

visualization can provide a powerful extension, supporting the visual evaluation of the simulated silvicultural treatments.

At present, marteloscopes are mainly used for training, and they provide a practical method to evaluate the perceptions and abilities of forest professionals and workers in forest tree marking (Vitkova et al. 2016). They can also be employed for specific research purposes, for example, studying the effects of innovative silvicultural treatments on the spatial structure of forest stands, where a wide variety of spatial indexes can be considered (Fabrika et al. 2018).

3.3 EuMIXFOR Empirical Contribution to Mixed Forests: Experimental Trials and Use of Different Datasets and Infrastructures

Scientific networking within the EuMIXFOR project offered the possibility to share research objectives and experiences and to plan joint studies after identifying gaps in mixed forest research. A road map was set out with the aim of creating a network for future collaboration. As an initial starting point, information on existing mixed forest experiments was gathered, e.g., number of experiments, species composition, or main purpose of the experiment. Some of the studies planned by this network required the establishment of comparable plots across Europe, applying a common protocol in order to draw general conclusions. Sharing of data, such as that collected as part of the EuMIXFOR project (Heym et al. 2017), was identified as being of particular value, not only to facilitate future comparisons but also to save time and money, avoiding duplicate data collection. A far-reaching proposal was put forward during the EuMIXFOR project with regard to establishing a worldwide network of triplets in mixed forests (Bravo et al. 2016). An initiative aimed at creating a common dataset of NFI data for various European countries has been developed for the study of certain characteristics of mixed forests.

3.3.1 Overview of Mixed Forest Experiments in Europe

Information from different European mixed forest experiments was compiled within the EuMIXFOR network by Working Group 1 ("Mixed forest dynamics and functioning"). A total of 88 mixed forest experiment designs were identified, covering 157 experimental sites across 17 European countries. This compilation includes mixed-species plantation trials, tree species diversity and proportion experiments, and silvicultural research plots. The information was compiled from literature as well

Table 3.1 Purpose of mixed forest experiments, number of experiments, and most frequent mixed forest types

Main purpose	Number of experiments	Number of sites
Growth	26	77
Management (thinning, conversion from pure to mixed forest, etc.)	26	35
Establishing mixed stands (regeneration, restoration, etc.)	25	30
Tree diversity experiments	6	8
Climate change adaptation	2	2
Not referred	3	5
All	88	157

Fig. 3.3 European countries with number of mixed forest experiments in the EuMIXFOR database (second number indicates the number of experimental sites)

as from a questionnaire on the current state of the art and drawn up by the EuMIXFOR Working Group 2 (“Adaptative management of mixed forests”).

Although the majority of the experiments have only recently been installed, a few were pre-existing long-term research experiments. This overview may not cover all the experiments, but it provides valuable insights into the types of experiment potentially available.

The number and main purpose of the experiments are presented in Table 3.1. In the majority of cases, the main purpose for installing an experiment was to study mixed forest growth-related topics ($n = 26$) and management ($n = 26$) of mixed tree species, although a combination of several different purposes was also reported.

In total, 37 experiments contained mixtures of 2 tree species, while 12 experiments included more than 5 tree species in different combinations. Although the majority of experiments contained only native tree species, 14 experiments included exotic tree species.

The most frequent type of two-species mixture comprised oak (*Quercus robur* L. or *Q. petraea* (Matt.) Liebl.) and European beech, with 13 experimental sites in total (11 concerned with growth-related aspects and 2 concerning conversion to mixed forests). Twelve experiments were composed of mixed conifer tree species, e.g., Scots pine and Norway spruce in four experiments and Norway spruce and Siberian larch in two experiments. The most frequent tree species was Norway spruce (37 experiments) followed by species of the *Quercus* genus (33 experiments). European beech was present in 29 and different pine species in 20 experiments.

The distribution of the mixed forest experiments in the 17 European countries contributing to this compilation is presented in Fig. 3.3. Over half of the experiments were located in the temperate climate zone ($n = 51$), 19 in boreal and 18 in the Mediterranean climate zone. Besides those mentioned above, there are other mixed forest experiments, both in the contributing countries and elsewhere in Europe, which have not been included in this compilation.

Some of the experiments listed originated in the TreeDivNet platform (www.treedivnet.ugent.be). For Northern Europe, the NOLTFOX platform (http://noltfox.metla.fi) can also be used to identify and locate additional long-term forest experiments listed under the category “tree species mixture.”

More detailed information on these experiments, including a list of the people to contact for each experiment, is provided in the final EuMIXFOR Working Group 1 report “European mixed forests – Integrating Scientific Knowledge in Sustainable Forest Management” (available at http://www.mixedforests.eu).

Although much effort is involved in establishing and continuously managing such experiments, the contribution as regards empirical research and the demonstration of pioneer work in forestry practices is of great value. However, due to their limited representativeness of site factors, it is not possible to draw general conclusions for important forest types at different sites. To draw more reliable conclusions, a combination (or at least a combined interpretation) with large-scale datasets, triplet studies, and different modeling approaches is required. To advance and apply the scientific knowledge to mixed forest management, the development of each of these research methods and concepts would benefit from the insights gained from another approach. Even though long-term experiments are likely to remain simply case studies, they still provide the best way to validate abstract models and challenge our ways of thinking in the future.

The experiments summarized here presented a broad scope of varying research questions and goals in their initial definition. However, as common research starts with a question, a jointly defined research question would provide a good starting point for using the experiments together. Thus, a few general ideas are shown below regarding the way in which existing mixed forest experiments could be used to address research questions highlighted by forest managers from different European countries and collected by Coll et al. (2018) as part of the EuMIXFOR project.

- Suitable silvicultural treatments which should be applied to maintain target species throughout the entire stand rotation. The need for silvicultural interventions could be analyzed depending on whether the tree species are more or less competitive.

- Appropriate species (or functional group) mixture in order to optimize specific or combined management targets (e.g., productivity, biodiversity, stability). An analysis could be applied to empirically explore the role of different components of biodiversity (tree species diversity, functional diversity) over long time periods.
- Knowledge of the effects of species mixture on wood quality can be very valuable for timber companies and land owners.
- Studies focusing on the expected balance of costs and benefits in pure versus mixed stands.

Data from long-term experiments could be used together with large-scale datasets to address the question of whether mixed forests are more resistant or resilient to climate change and natural disturbances than monocultures.

One strength of the mixed forest experiments is that they can provide temporal validity if long-term observations are available. In addition, it is easier to control and measure the direct competition between trees in forest experiments in comparison to data from large-scale inventories. Furthermore, ring width data is usually only available from the experiments, as the collection of such data is not planned in large-scale inventories or at least only a sample is collected.

A weakness of the mixed forest experiments tends to be their lack of representativeness due to the small size of the plots (between 0.1 and 1 ha). Therefore, mixed forest experiments may be not suitable for some cross-scale biodiversity research, for example, if mobile animal species are the focus of the study. Also, cost estimates derived from the existing experiments have drawbacks: forest operations in experiments are more carefully carried out than under normal conditions.

Finally, scarce information is available on the underlying mechanisms and tradeoffs associated with the mixing effects. Therefore, the efficiency of mixed tree species in the used resources (light, water, nutrients) compared to monospecific stands would need to be empirically tested in the experiments and used to validate different physiological models. For these purposes, a more intensive data collection should be carried out in the mixed forest experiments, extending the sampling to measure soil conditions, transpiration rates, morphology, light interception, etc.

3.3.2 Triplet Initiative Along a Stand Productivity Gradient in the Mixture of European Beech and Scots Pine

To understand and generalize the processes underlying forest stand productivity, data from different growing conditions are required. Permanent forest research plots provide an adequate, detailed empirical database when following standardized protocols, e.g., DESER-Norm (Johann 1993). In mixed forest research, to study the effects of mixing tree species, monospecific stands of the different species in the mixture are important as references, but they are not always available. Permanent mixed plots are not only limited in number but also costly to maintain and tend to be linked to specific aspects of research. Moreover, there may be no plots at all for many combinations of tree species or gradients of growing conditions. Temporary plots can serve as an ad hoc alternative to cover such gaps. In principle, only one survey is required, although this necessarily involves a stand-specific reconstruction of its recent development based on increment cores.

Under the umbrella of the EuMIXFOR project, an initiative was launched to set up a network of temporary plots in Europe. For the first time, 32 triplets for investigating the mixture of European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) across a productivity gradient were established following a standardized protocol (Heym et al. 2017). One triplet comprises two monospecific stands (species A and B) and one stand with a mixture of the two species, all with similar climatic and soil conditions (Pretzsch et al. 2015; Thurm et al. 2016; Wellhausen et al. 2017). All the plots represent predominantly even-aged, fully stocked stands and monolayered forests, being similar in age. Figure 3.4 shows the

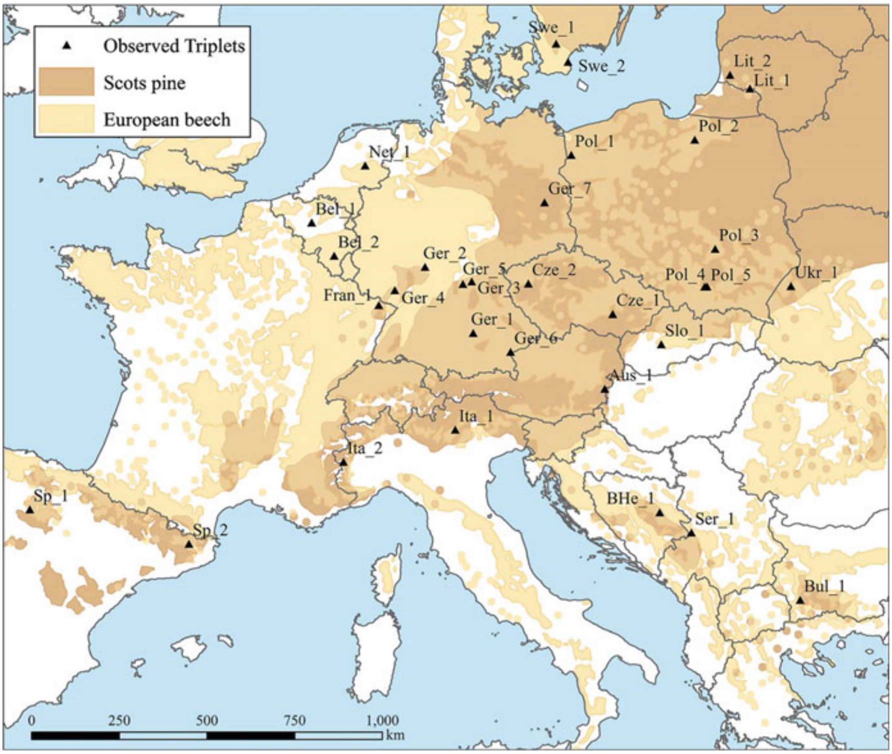

Fig. 3.4 Distribution of the triplet locations across Europe and distribution of European beech and Scots pine according to EUFORGEN (http://www.euforgen.org). Triangles represent triplet locations. Labels refer to triplet number per country and country names: *Ger* Germany, *Pol* Poland, *Bel* Belgium, *Cze* Czech Republic, *Ita* Italy, *Lit* Lithuania, *Sp* Spain, *Swe* Sweden, *Aus* Austria, *BHe* Bosnia and Herzegovina, *Bul* Bulgaria, *Fran* France; *Net* The Netherlands, *Ser* Serbia, *Slo* Slovakia, *Ukr* Ukraine

triplet locations across 16 European countries. During the triplet initiative, 96 plots (32 triplets), comprising 7555 trees, were sampled.

Standardized methods, developed during the EuMIXFOR project, allow the reconstruction of stand characteristics at plot level for a period of approximately 10–15 years back in time. Following a three-step procedure, the recent growth in diameter at breast height (dbh), stem height (Kennel 1972; Franz et al. 1973), and merchantable volume over bark (Franz 1971) of each tree was determined. The reconstruction starts with the dbh, by fitting OLS (ordinary least squares) regression models that describe the relationship between tree diameter and its increment as determined from the increment cores for a given period of time per plot and species.

A set of 15 plot and tree-specific mandatory dendrometric attributes were measured in each plot, including the diameter at breast height, total height, and height to crown base of each tree. In addition, for the majority of the plots, tree positions and crown radii were also recorded (Table 3.2). For a subsample of 4695 trees, increment cores were taken, representing the range of the diameter distribution per plot and species.

For all non-cored trees in the stand, their retrospective diameter development can be calculated by applying these plot and species-specific models. Individual tree heights can be calculated based on the reconstructed dbh, e.g., following the methodology based on a uniform height curve system developed by Kennel (1972) and extended by Franz et al. (1973). In addition to the individual tree

Table 3.2 Overview of measured mandatory and optional descriptive and dendrometric attributes

Type	Variable	Description
Mandatory	Longitude	Plot specific
	Latitude	Plot specific
	Altitude	Plot specific; m (E. a.s.l.)
	Slope	Plot specific; degrees
	Aspect	Plot specific; degrees
	Plot size	Plot specific; hectares
	Date of establishment/ measurement	Triplet specific; yyyy-mm
	Age	Species and plot specific; years
	Tree number	Living trees; ascending order
	Tree species	Scientific species name
	Diameter at breast height	Tree specific (cm)
	Tree height	Tree specific (m)
	Crown base height	Tree specific (m)
	Increment cores	2 core samples/tree, 10–20 trees/plot/species
	Local density	1–2 angle count measurements/cored tree; m^2 ha^{-1}
Optional	X-coordinate	Tree specific (Cartesian)
	Y-coordinate	Tree specific (Cartesian)
	Crown radii	Tree specific; azimuth (degrees) and distance (m)

diameters, this system requires the stand age, quadratic mean diameter, and its corresponding height as inputs. While the former are easy to reconstruct, the latter has to be estimated on a plausible basis, for example, using yield tables for Scots pine (Wiedemann 1943) and for European beech (Schober 1967). With reconstructed tree-specific diameter and height time series, species-specific form factors, such as provided by Franz (1971), allow the merchantable volume over bark for individual trees to be calculated. Time series of stand characteristics can be reconstructed following DESER-Norm, for example (Johann 1993).

From a methodological perspective, the initiative showed that triplets provide an alternative to permanent research plots with respect to recent stand development and productivity. Therefore, the concept can be recommended for further systematic research into the effects of tree species mixtures. Recent research has already broadened the usage of such triplets of Scots pine and European beech, for instance, Pretzsch et al. (2015) showed that mixtures of these species were approximately 12% more productive (stand volume). Pretzsch et al. (2016) also found that structural heterogeneity increases in these mixtures in comparison to monocultures and that the mixing effects are linked to both species identity (different traits) and species interaction. Dirnberger et al. (2017) analyzed the different methodologies and determined that the best method to describe species proportion at stand level was the one that relates the observed density to its potential, taking into account climatic conditions for potential densities. At tree level, the methodology considering crown projection area or leaf area was determined to be the best. Forrester et al. (2017) analyzed the effects of mixing on growth and yield for these triplets and compared them with predicted effects from the 3-PG model in order to determine the accuracy and relevance. Forrester et al. (2018) also reported that absorption of photosynthetically active radiation is 14% higher in mixtures compared to monocultures and that the magnitude of this mixing effect was positively correlated with site productivity, canopy volume, and canopy depth, but not with climatic variables. del Río et al. (2017) found that species mixing stabilizes productivity at community level, whereas it has a neutral or negative effect on stability at population and individual tree levels. Additionally, these authors point to temporal niche complementarity between species as the key driver in the stabilizing process. The data from these 32 triplets (stand and ring width data) are available at https://doi.org/10.5061/dryad.8v04m (Heym et al. 2017).

Triplet methodology is not new. It has been used in the study of different species mixtures in various studies concerning, for example, Norway spruce and European beech (Pretzsch et al. 2010) or oak and European beech (Pretzsch 2013; Pretzsch et al. 2013) using data from long-term permanent plots. This methodology can be used to study the general response of different mixtures to the variation in an environmental factor. Such experiments already exist across a worldwide research network of mixed forest triplets (see next section). This approach can also be used to determine the response of specific mixtures along an environmental gradient. Hence, within the framework of the REFORM project (www.reform-mixing.eu), a network of Scots pine and oak triplets as well as Scots pine and Norway spruce triplets has been established in European forests in order to study these mixtures. The main purpose of this project is to analyze the resilience of forest mixtures and also to identify the effects of thinning on mixed forests.

3.3.3 Worldwide Forestry Research Network of Mixed Forest Triplets

As an extension of the EuMIXFOR triplet initiative (for studying European beech and Scots pine mixture), an international group of scientist around the world is currently establishing a new network of triplets (Bravo et al. 2016), comprising species with different stress tolerances (mainly shade tolerance). The species represented in the mixtures include examples from boreal, temperate, Mediterranean, and tropical forests (Table 3.3). In all cases, the stands selected are close to the maximum mean annual increment (MAI) age, except for the *Picea abies* (L.) H. Karst.-*Larix decidua* Mill. and *Pinus durangensis* Mtz.-*Pinus arizonica* Engelm. mixtures, where stands close to the maximum current annual increment (CAI) were chosen (for MAI and CAI clarifications, see, e.g., Assmann 1970 pp. 80; Pretzsch 2009 pp. 397–398). Data gathering was based on tree coring at each triplet with the exception of the Chilean triplets (see Table 3.3), where data were based on longitudinal mensurative experiments (permanent plots). Data acquisition from this network is planned to finalize during 2018.

3.3.4 Data from National Forest Inventories

In order to cover a greater range of environmental conditions, large datasets can be used to test different hypotheses related to functioning, productivity, or management of mixed forests. During the EuMIXFOR project, five European countries (Austria, France, Germany [data for Bavaria], Poland, and Spain) provided data from their NFIs to create a common dataset to study productivity in mixed and monospecific stands of Scots pine and European beech and its variation with site environmental conditions. The dataset consists of stand variables (dominant height, quadratic mean diameter, number of stems per ha, basal area growth, both total and per species) from plots located in monospecific stands of Scots pine (9.683 sample plots) and in monospecific stands of European beech (2.881 sample plots) and mixtures of both species (609 sample plots) (Fig. 3.5). The database also includes site information (longitude, latitude, and altitude above sea level), annual precipitation, and mean annual temperature for all recorded sample plots. The Martonne aridity index (Martonne 1926) was also calculated from these climatic variables. As a first step in the calculation of species proportion and stand density in mixed stands, a study of maximum size-density relationship (MSDR) of Scots pine and European beech was developed. The results showed that the species' boundary lines of maximum density

Table 3.3 Planned triplets in different species mixtures (worldwide network)

Shade tolerant species	Shade intolerant species	Geographical area
Fagus sylvatica L.	*Pinus sylvestris* L.	Europe (EuMIXFOR network)
Pinus nigra Arn.	*Pinus sylvestris* L.	Spain
Pinus sylvestris L.	*Pinus pinaster* Ait.	Spain
Quercus pyrenaica Wild.	*Pinus sylvestris* L.	Spain
Quercus pyrenaica Wild.	*Pinus pinaster* Ait.	Spain
Fagus sylvatica L.	*Pseudotsuga menziesii* (Mirb.) Franco	Germany
Picea abies (L.) H. Karst.	*Pinus sylvestris* L.	Germany
Fagus sylvatica L.	*Picea abies* (L.) H. Karst.	Germany
Picea abies (L.) H. Karst.	*Larix decidua* Mill.	Germany
Fagus sylvatica L.	*Quercus petraea* (Mattuschka) Liebl.	Belgium
Quercus petraea (Mattuschka) Liebl.	*Pinus sylvestris* L.	Poland
Pseudotsuga menziesii (Mirb.) Franco	*Alnus rubra* Bong.	Oregon (USA)
Tsuga heterophylla (Raf.) Sarg.	*Acer macrophyllum* Pursh.	Oregon (USA)
Nothofagus nervosa (Phil.) Krasser	*Nothofagus obliqua* (Mirb.) Oerst.	Argentina
Nothofagus dombeyi (Mirb.) Oerst.	*Nothofagus obliqua* (Mirb.) Oerst.	Argentina
Swietenia macrophylla King	*Samanea saman* (Jacq.) Merr.	Costa Rica
Quercus humboldtii	*Pinus patula* Schied. ex Schltdl. & Cham.	Colombia
Quercus falcata Michx.	*Fraxinus excelsior* L.	Chile
Sorbus torminalis (L.) Crantz.	*Pyrus pyraster* Borkh.	Chile
Quercus falcata Michx.	*Prunus avium* (L.) L.	Chile
Juglans regia L.	*Prunus avium* (L.) L.	Chile
Quercus robur L. and *Quercus rubra* L.	*Prunus avium* (L.) L. and *Castanea sativa* Mill.	Chile
Pinus durangensis Mtz.	*Pinus arizonica* Engelm.	Mexico
Podocarpus falcatus (Thunb.) R. Br. ex Mirb.	*Juniperus procera* Hochst. ex Endl.	Ethiopia

are climate-dependent and that the pattern of variation was species-specific (Condés et al. 2017). The same conclusion was reached in a study involving five different pine species across the climatic gradient of the Iberian Peninsula (Aguirre et al. 2018). Both studies used the MSDRs developed for monospecific stands to discuss the relevance of humidity for the competition equivalence coefficients in mixtures.

High environmental variability in NFI plots over large areas can capture the variation in the role of functional and structural traits in the maximum stocking of pure and mixed stands. Ducey et al. (2017), using data from the US Forest Inventory and Analysis program, and Bravo-Oviedo et al. (2018), based on data from the

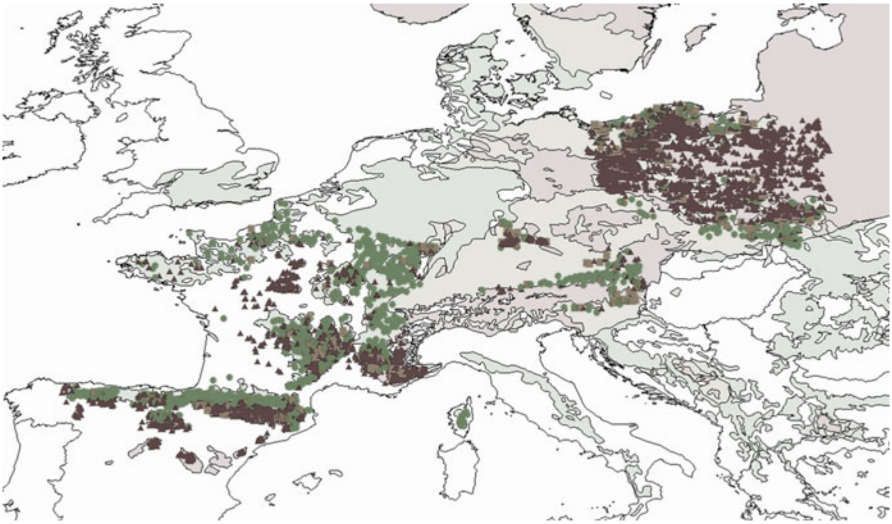

Fig. 3.5 NFI plot locations for monospecific pine stands (triangles, red), monospecific beech stands (circles, green), and mixtures (squares, brown)

Spanish NFI, confirmed the role of tolerance to drought, shade, and bending stress as modulated by climate in the determination of maximum stand density.

During the EuMIXFOR project, Dirnberger et al. (2017) used the climate-dependent MSDR to estimate species proportions in some of the triplets established in mixed and monospecific stands of Scots pine and European beech in the transect study initiative (see Sect. 3.3.2). They concluded that stand-level estimation of species proportions, based on the climate-dependent maximum density lines, provided a better approach than species proportions estimated at tree level using the species leaf areas.

In accordance with this finding, the climate-dependent MSDR lines were used to calculate species proportion for all plots in the NFI database (Condés et al., in preparation). Stand basal area growth models for Scots pine and European beech along the gradient of site conditions in Europe were then developed. In a first step, the models were fitted using all available data from monospecific and mixed stands, the results obtained pointing to a positive mixing effect for basal area growth in beech, whereas in the case of pine, the effect shifted from negative to positive depending on the humidity (Fig. 3.6).

In a second step, since there was clearly an imbalance between the number of plots in monospecific stands and those in mixed stands and that this could affect the results, the models were refitted using only a subset of the same number of plots in monospecific and mixed stands, both in locations with similar site conditions. These are termed pseudo-triplets. The same mixing effects, although slightly more pronounced, were obtained from these new models. Both models were validated using data from the triplets established during the EuMIXFOR project, and it was found that the use of pseudo-triplets slightly improved the models (Fig. 3.7), the results

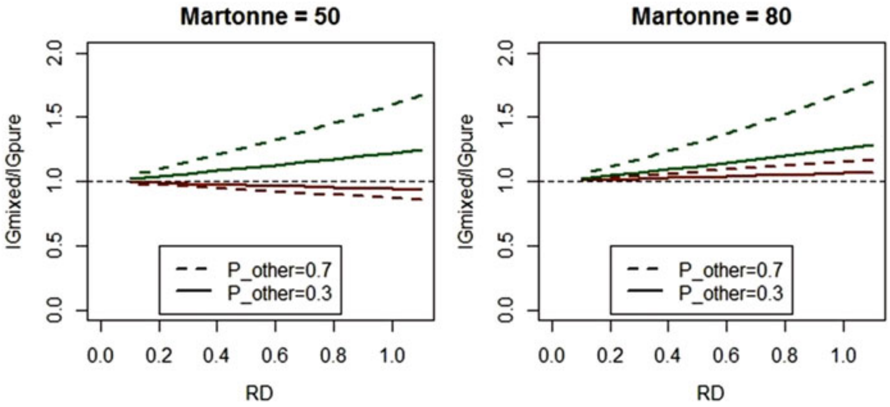

Fig. 3.6 Ratio between basal area growth in mixed (*IGmixed*) and monospecific stands (*IGpure*) versus relative density (*RD*) for two contrasting humidity conditions. Red lines for Scots pine and green lines for European beech. Solid lines for proportion of competitor species equal to 0.3 and dashed lines for proportion equal to 0.7

being aligned with the triplet data (Condés et al. 2016). However, the selection of pseudo-triplets can be affected by a level of subjectivity, given the impossibility of controlling site conditions in NFI plots. Therefore, a further analysis is necessary to assess the degree of uncertainty associated with the selection of pseudo-triplets (Condés et al., in preparation). NFI plots cover almost all the range of variability of mixed stands, although stand conditions are weakly controlled. Another strength is that mixing effects are better reflected in NFI plots than in transect plots due to the great variability of the mixture and the limited number of transect plots. The analysis of NFI data can complement the results obtained from transect plots. For example, the mixture effect pattern in the beech-Scots pine study could be identified from NFI data but not from transects plot data.

3.4 Concluding Remarks

We have gathered most of the existing European mixed forest experiments under the umbrella of the EuMIXFOR project. These forest experiments, together with data from forest inventories and exploratory data, contribute to our understanding of mixed forest functioning and development.

The main contribution of EuMIXFOR to the data platforms for the study of mixed forest is the European triplet initiative for studying European beech and Scots pine. This study was planned and carried out within this network. For this purpose, common plot establishment and measurement protocols were agreed with the EuMIXFOR participants in order to homogenize data collection. Although a number

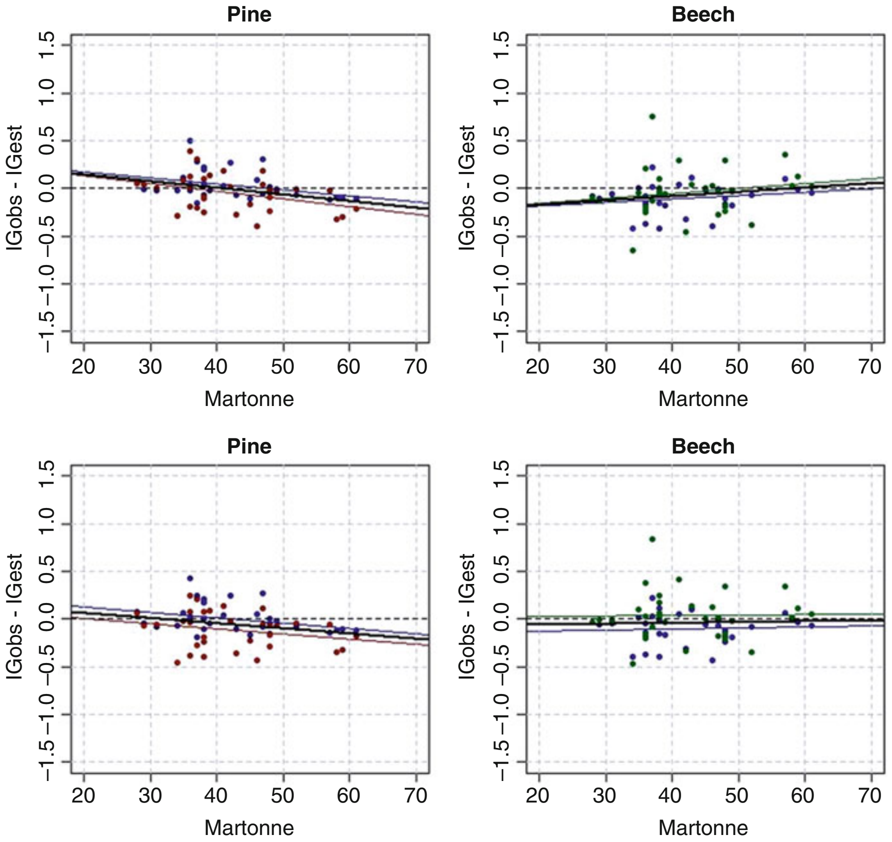

Fig. 3.7 Evaluation of models using the EuMIXFOR triplets. Top: models developed using all available data. Bottom: models developed from pseudo-triplets. Red and green points corresponding to pine and beech monospecific plots, respectively. Blue points corresponding to mixtures

of studies have already been conducted, the availability of data from these triplets means that other research questions can now be addressed.

Another milestone achieved under the EuMIXFOR project, following the same idea as the beech-pine study, has been the development of a worldwide network of triplets based on species stress tolerance. As other joint contribution, a common dataset of NFI data for various European countries has also been established to study some of the important admixtures.

As regards silvicultural research in mixed forests, Pretzsch and Zenner (2017) have identified certain future necessities that could be incorporated into future experimental designs. These include direct effects of mixing in order to identify the effect of different species proportion, mixing patterns, or age structures; morphological changes in trees (tree shape, allometry, stem form factor, etc.); structure effect on species identity and structural traits of the stand; scale of experiments;

multiple ecological gradients; other yield components apart from productivity (such as height, diameter, mortality, regeneration, etc.); wood quality; trade-offs; provision of other ecosystem services; exploring temporal mixtures of species; exploring a decrease in the application of silvicultural treatments due to declining budgets; defining management success; etc. Initiatives such as EuMIXFOR could help to address these future research needs.

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Chapter 4
Regeneration Patterns in Mixed-Species Stands

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Abstract Mixed forests have been proposed as a tool for more flexible wood production that simultaneously improves conditions for biodiversity and various social demands. Therefore, regeneration of mixed forests has become an important topic of practical concern throughout the world. Here, we briefly review important ecological processes in the early phases of stand development. In addition, we review the various regeneration techniques that can be used, i.e., natural and artificial regeneration of mixtures. Our paper highlights some important knowledge gaps for improved management of young mixed-species stands in Europe. For example, few studies have addressed the specific seed production conditions in mixed forests. Thus, even if some management recommendations can be given for mixed-species regeneration, predicting natural regeneration in mixed stands is problematic. Generally, it is more complicated to formulate rules for young mixed stand development than for monocultures. Much species-specific knowledge is still lacking regarding responses to interactions, although from a management perspective, it seems easier to manage mixtures groupwise rather than stem-wise. Finally, we highlight high deer

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populations as perhaps the greatest challenge for mixed forest regeneration. More knowledge in the field and greater cooperation between researchers and different stakeholder groups are needed to solve this problem.

4.1 Introduction

The world forests are subjected to increasing pressure from a growing human population, and in some parts of the world, natural forests are still converted to grazing lands or other agricultural uses (Minnemayer et al. 2011). In addition, global change is causing a high degree of uncertainty concerning future ecological and environmental conditions (Stanturf et al. 2014; Jacobs et al. 2015). Mixed forests have been proposed as one tool to tackle this situation and in addition to a more flexible wood production simultaneously improve conditions for biodiversity conservation and various social demands and provide management flexibility for an uncertain future (Paquette and Messier 2013; Verheyen et al. 2016; Bravo-Oviedo 2018). The tree regeneration phase offers the best opportunity to influence tree species composition and forest ecosystem structure. More multipurpose and mixed forests may also help preserve the world's remaining primary forests. Therefore, regeneration of mixed forests has become an important topic of practical concern throughout the world. However, there is much less scientific and practical information concerning regeneration, establishment of young stands, and early management in mixed-species stands compared to monocultures (Pretzsch et al. 2017).

Mixed-species stands are more complex than monocultures (Del Río et al. 2018). The larger genetic variability of mixtures results in a large variation in growth rates, between tree species but also between individuals of the same tree species, and the environment in mixed-species stands is more heterogeneous compared to monocultures. This is partly because mixtures more often rely on natural regeneration (which is more variable) compared to monocultures which primarily are created by artificial regeneration but also due to the fact that the different tree species affect the above- and belowground environment in different ways. While mixed regeneration has been identified as an important tool for adapted forest management to climate change and for forest restoration, the greater complexity in mixed plantations that results from interspecific interactions requires more knowledge.

This chapter focuses on the regeneration of mixed-species stands. We briefly review important ecological processes in the early phases of stand development. These are seed production, dispersal of seeds, competition, facilitation, and shade tolerance. In addition, we review the various regeneration techniques that can be used, i.e., natural and artificial regeneration, and analyze the challenge that high populations of browsing animals (deer) bring to the objective of regenerating mixtures. Most of our literature covers European conditions. We relate the knowledge to the four-stage model of stand dynamics proposed by Oliver and Larson (1996). By doing so, we attempt to fill some of the relevant knowledge gaps that exist in this subject, highlight others, and finally discuss future research needs. We hope that our conclusions will stimulate the development of new management guidelines for regeneration of mixed-species stands.

4.2 Stand Dynamics and the Possibilities of Establishing Mixtures

Many forests around the world develop in similar ways following major disturbances such as fire, wind, or clear-cuts (Oliver and Larson 1996). Here, mixed-species stands have the same dynamics as single-species stands although mixtures contain much more variation and are more complex. Different authors have named the different stages of stand development following a major disturbance differently, but here we follow Oliver and Larson (1996) who differentiated between stand initiation (1), stem exclusion (2), understory reinitiation (3), and old multi-aged community (4) (Fig. 4.1). Following the disturbance, many trees begin growing in the open space from seed, sprouts, or advanced regeneration. In this first "stand initiation" stage, the stand is characterized by one or just a few regeneration cohorts or age classes. Typically some light-demanding tree species grow faster than other more shade-tolerant tree species. The number of tree species depends on the composition of seed sources in the surroundings and on the amount of sprouts and advanced regeneration. The stand structure changes once the trees have occupied the site, and inter- and intraspecific competition starts to become intense. In the "stem exclusion" stage, mortality is high, and the canopy is too dense to allow new

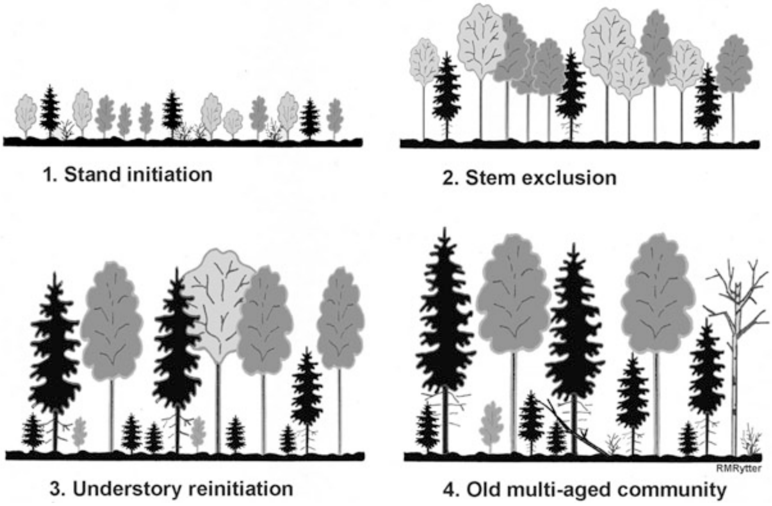

Fig. 4.1 Schematic illustration of a four-stage model of stand dynamics after Oliver and Larson (1996). (Drawing: Rose-Marie Rytter)

regeneration to develop in the understory. Only a few age classes occur in the canopy which is dominated by faster-growing trees or trees that initially had a superior crown position. As trees grow taller and a larger variation in tree heights and diameters occurs, the tree crowns become so large that they cannot immediately fill gaps that occur after the death of trees. This is called the "understory reinitiation" stage since the gaps allow more light to reach the ground and, thus, new regeneration of trees can develop in the understory. Normally this new regeneration is dominated by more shade-tolerant tree species. In the absence of new major disturbances, stands may develop into the "old multi-aged community" stage. This is characterized by mortality of large trees and further gap creation that allows recruitment of some individuals from the regeneration into the canopy. This creates more variation, an irregular structure, and the presence of large dead trees. The possibility to create new mixtures is highest in the first and third stage of this four-stage model of stand dynamics. Stands in the second stage are normally too dense and dark to allow any new regeneration, and the tree composition cannot be changed. Stands in the fourth stage are not very common in Europe, and when occurring many times set aside for conservation purposes.

4.3 Ecological Processes Applicable to the Regeneration of Mixed-Species Stands

4.3.1 Seed Production and Dispersal

Pollination, flowering, and seed production trigger the regeneration cycle (Harper 1977; Fischer et al. 2016), but only a few studies have focused on the specific seed production conditions in mixed forests and the preceding development processes (Müller-Starck and Schubert 2001; Wesołowski et al. 2015; Bogdziewicz et al. 2017). In mixed forests, the temporal and spatial synchrony of flowering and fruiting of trees influence (1) the future genetic constitution within and among tree populations, (2) the regeneration success, and (3) the maintenance of tree species admixtures (Yazdani and Lindgren 1992; Liebhold et al. 2004; Hosius et al. 2006; Moran and Clark 2012; Nussbaumer et al. 2016). Tree species are characterized by individual inflorescences (mon-, di-, or trioecious) and related pollination mechanisms (Pearse et al. 2015). Many Northern Hemisphere tree genera (e.g., *Betula*, *Quercus*, *Fagus*, *Pinus*, *Picea*) are wind-pollinated (anemophilous) and thus strongly influenced by wind speed or wind direction. Further effects are caused by local or regional climate conditions such as temperature or precipitation during different key periods (Satake and Iwasa 2002; Pearse et al. 2015; Vacchiano et al. 2017). By comparison, another group of tree species (e.g., *Acer*, *Sorbus*, and *Tilia*) depends on the presence, behavior, and mobility of insects as pollen vectors (Anderson 1976; Pigott and Warr 1989; Raspé et al. 2000; Pigott 2012). Weather conditions, resource availability, and predator satiation – among others – can affect pollination, flowering, and fruiting success (Kelly 1994; Müller-Starck and Stimm 2007; Pérez-Ramos et al. 2014; Wesołowski et al. 2015; Bogdziewicz et al. 2017). It can be assumed that these factors are the relevant drivers to fruit production in mixed stands too (Geburek et al. 2012; Nussbaumer et al. 2016). However, depending on the pattern of the mixture, instances between conspecifics for pollen exchange can be larger, and the synchrony of fruiting years of different species is rarely given (Shibata and Nakashizuka 1995) in mixed stands.

Supported by genetic analyses, the mean distances of wind-dispersed pollen grains can range between 20 and 5000 m (Yazdani and Lindgren 1992; Piotti et al. 2012; Gerber et al. 2014; Holderegger et al. 2015), whereas mean pollen dispersal distances of insect-pollinated species range between 5 and 750 m (Kevan and Baker 1983; Dick et al. 2003; Jong et al. 2005; Oddou-Muratorio et al. 2005). For both pollination types, distance-dependent models illustrate the rapid decrease of pollen density for distances more than 250 m from the sources (Austerlitz et al. 2004; Dobeš et al. 2017). As a consequence, the efficiency and the success of pollen dispersal can be reduced between fragmented forest areas, admixed isolated trees, or low densities of mature conspecific trees (Robledo-Arnuncio et al. 2004; Pearse et al. 2015).

Furthermore, the process of flowering and the total number of seeds produced depend on the physiological age and the onset of maturity in the trees (Owens and Blake 1985; Wenk and Falster 2015). In most cases the maturity of free-standing trees or trees that experience optimal resource availability (e.g., nutrients, water) starts at a younger age than in closed forest conditions (Pérez-Ramos et al. 2014; Wenk and Falster 2015). Many studies have shown that relevant processes driven by environmental conditions are difficult to control, but the vitality of seed trees and therefore the amount of seeds can be supported by silvicultural measures. Especially in intensive tree species admixtures (single trees up to small groups), the vitality of individual trees depends on their hierarchical position and competitive situation within heterogeneously structured forests (Mund et al. 2010). In that respect, single-tree-oriented thinning from above encourages the vitality of dominant trees and increases the development of crown dimensions and stem diameters (Mäkelä and Valentine 2006). Positive allometric relations between crown surface, stem diameter, and the amount of produced seeds are well proven for different tree species and utilized in seed tree systems (Gysel 1957; Greene and Johnson 1994; Bellocq et al. 2005; Rodríguez-Calcerrada et al. 2011; Karlsson 2000; Rose et al. 2012; Martiník et al. 2014). To enhance the seed production of target tree species in mixed forests by the regulation of crown competition, it is necessary to consider the species-specific shade tolerance and the potential of crown expansion of mature trees. Especially for *Pinus*, *Quercus*, *Acer*, and *Betula*, rigorous release thinning oriented to the light crown part must be ensured. These tree species are characterized by a low tolerance of crown competition, low crown plasticity, and the fact that seeds are exclusively located in the upper light crown (Karlsson 2000; Olson et al. 2015).

Diverse environmental factors determine the simultaneous or subsequent presence of seed consumers or predators. Seeds can be damaged in the crown by insects or fungal diseases before ripening and dispersal. Large seeds of *Quercus*, *Fagus*, or *Juglans* are more attractive for rodents or highly specialized birds, e.g., jays (Bossema 1979; Jensen 1985; Bell and Clark 2016). In pure forest stands, seed losses caused by predators can reach high proportions, but this is offset by the large number of seeds during masting events, described as "predator satiation hypothesis" (Kelly 1994). The assessment of seed predation within mixed compared to pure forests needs further analysis of different stand structures (Hoshizaki and Miguchi 2005).

The few seconds or minutes of flight, fall, or transport of a seed after release from the parent tree are a unique period of movement in the life cycle of a tree. This movement causes implications for the gene flow system of the species (Gerber et al. 2014); it is a central contribution to the migratory capability of a species (Clark 1998); and it can take the individual away from immediate competition, i.e., from the parent tree and the siblings (Janzen 1970) to a variety of sites or environments. Due to the enormous importance of this process to the fate of the individual and to the adaptability and adaptedness of the entire species, trees have developed specific dispersal strategies, e.g., the agents of dispersal are specific, and the distances the seed travel are very diverse (from some meters to kilometers) (Table 4.1). We distinguish "anemochory" (wind mediated in, e.g., *Picea*, *Acer*), "zoochory" (animal mediated in, e.g., *Pinus cembra*, *Quercus robur*), and "hydrochory" (water mediated in, e.g., *Alnus*, *Fraxinus*) besides "barochory" (gravity mediated in, e.g., *Fagus*). A very general difference between the anemochorous, hydrochorous, and barochorous systems on one hand and the zoochorous system on the other hand is in the feature of chance. Whereas in the former systems we may assume the probability of seed arrival in particular environments is chance driven, i.e., "seed rain" (Shibata and Nakashizuka 1995; Houle 1998), zoochorous systems often show the feature of "directed dispersal" (Bazzaz 1991; Wenny 2001; Briggs et al. 2009) to preferred habitats or environments of the animals.

As the probability of seedling establishment increases with increasing density of seeds (Nyland 2002), the distance of dispersal from a parent tree and the habitat the seed arrives are decisive for regeneration success. The feature of distance is particularly relevant in barochorous and anemochorous species, as these dispersal mechanisms unavoidably cause decreasing seed densities with increasing distance to the seed tree. An exception to this rule may occur in species with plumed seeds like willows or poplars (Schirmer 2006; Gage and Cooper 2005).

In some zoochorous species, the animals carrying the seeds may cover large distances until they find a habitat that suits their requirements. This is particularly true in scatter hoarders like the jays (Gómez 2003). However, in endozoochorous species, e.g., cherries or apples and pears, the dispersal distance depends on the duration of the gut passage (Fedriani et al. 2010) and to a lesser extent on the habitat preferences of the animals.

Much work has been done on the modeling of seed dispersal (e.g., Ribbens 2002; Wälder et al. 2009; van Putten et al. 2012). We may differentiate between "mean dispersal distance" (MDD) and "long dispersal distance" (LDD), as these distance measures have different relevance in silviculture for timber production compared with scenarios considering ecology of invasion. As long as foresters aim for high seedling densities to secure regeneration and to improve the timber quality of the

Table 4.1 Overview of seed dispersal mechanisms and dispersal distances for different genera of European trees

Genera	Seed dispersal mechanisms	Mean dispersal distances (m)	References
Broadleaves			
Acer	Anemochorous	35–85, 26–130	Diaci et al. (2001) and Schütt et al. (2002)
Alnus	Anemochorous, hydrochorous	30–60	McVean (1955)
Betula	Anemochorous	50–192, 40–100, 25–92	Sarvas (1948), Karlsson (2001, 25–92), and Huth (2009)
Carpinus	Anemochorous	24–73, <130	Kohlermann (1950) and Bouman et al. (2000)
Fagus	Barochorous, zoochorous	6–12, 20–30, rodents 4, birds 32	Kutter and Gratzer (2006), Diaci et al. (2001), Jensen (1985), and Müller-Schneider (1949)
Fraxinus	Anemochorous, hydrochorous	39–88, 47–66, 14–49, river 970 m year^{-1}	Wagner et al. (2004), Schmiedel et al. (2013), Heuertz et al. (2003), and Thébaud and Debussche (1991)
Quercus	Barochorous, zoochorous	Rodents 15, jay 263, jay 68	Jensen and Nielsen (1986), Gómez (2003), and Pons and Pausas (2007)
Sorbus	Zoochorous	<50	Asche et al. (2007)
Tilia	Anemochorous	19–64	Kohlermann (1950)
Ulmus	Anemochorous	<30	Venturas et al. (2014)
Conifers			
Abies	Anemochorous	22–44, 6–11, 10–22	Kutter and Gratzer (2006), Paluch (2011), and De Andrés et al. (2014)
Larix	Anemochorous	29–38	Kohlermann (1950)
Picea	Anemochorous	4–17, 35–51, 39–57, 345	Dovčiak et al. (2008), Kohlermann (1950), Kutter and Gratzer (2006), and Piotti et al. (2009)
Pinus	Anemochorous	20–50, <30	Kellomäki et al. (1987) and Mukassabi et al. (2012)
Pseudotsuga	Anemochorous	60, <20	Isaac (1930) and Tschopp et al. (2015)

new generation, the MDD seems most relevant for assessing the appropriateness of the density and spatial pattern of seed trees to regenerate a stand. See Table 4.1 for examples of dispersal mechanisms and distances for different genera of European trees species.

When pure stands are to be regenerated to establish mixtures using natural regeneration (e.g., in restoration, see Fischer et al. 2016), the distance to parent trees of the additional species is relevant in anemochorous species. In zoochorous species, the suitability of the pure stand as a habitat for the seed-dispersing animals is of importance. Young pine stands (e.g., stem exclusion stage, see Stähr and Bergmann 2006) (Fig. 4.1) seem not appropriate for the jay to place acorns; but somewhat older pine stands are.

In mixed stands, parent trees of different species may not be distributed regularly, and clumped or random patterns of mixtures may occur. The proportions of the species may also vary, and specimens of rare species may occur as single trees in a stand. These different patterns cause a variety of seed densities of a particular species within a stand.

4.3.2 Competition, Facilitation, and Shade Tolerance

While regeneration of mixed-species stands has gained more interest during the last decades, the greater complexity in young mixed stands that results from interspecific interactions requires more knowledge. Species interactions, both negative and positive, are key components of forest dynamics since they are often at the origin of species coexistence and replacement processes (Goldberg and Barton 1992). Negative interactions (interspecific or intraspecific competition) occur when the simultaneous demand by different species or individuals for growing resources produces a negative effect on the survival, growth, or reproduction of the other species or individual (Begon et al. 1996). Positive interactions (facilitation), in contrast, occur when at least one species enhances the survival, growth, or reproduction of another (Callaway 2010). This could be mediated by different mechanisms such as protection from the impacts of herbivores, environmental extremes, or other competitors (Brooker et al. 2008). The positive effects of one species on another could also be related to the reduction of the competition experienced by the latter when growing close to the first (i.e., when interspecific competition for an essential resource is less than intraspecific competition). In mixed forests, competitive reduction and facilitation effects occur frequently and are difficult to separate. Then, they are often collectively described as complementarity effects (Forrester 2014). Any management action to create mixtures, either by means of promoting natural diversification of established pure stands or by artificially planting (or direct seeding), needs to consider the competitive ability of the species involved and the expected outcomes of their interactions. The competitive ability of a species can relate to its capacity to capture more resources than another (or to use them more efficiently) but also to its higher ability to survive (or growth) under the stress associated with low resource levels (e.g., shade tolerance or drought resistance) (Valladares and Niinemets 2008).

Natural diversification processes in pure secondary forests start in general once trees have closed canopy (stem exclusion stage, Oliver and Larson 1996) and intensify during the next stage (understory reinitiation) when the canopies begin to open as trees become older. During the stem exclusion phase, some shade-tolerant species are able to establish in the understory and benefit from the protection conferred by the canopy cover from high temperatures and soil moisture depletion (direct facilitation) (Caldeira et al. 2014) and from the canopy's control of competing vegetation (indirect facilitation) (Pagès et al. 2003; Kunstler et al. 2006). This nurse effect of the canopy layer is frequently observed in Mediterranean areas, where, e.g.,

Fig. 4.2 Natural diversification of planted *Pinus nigra* stands established in ancient agricultural fields by two different oak species (*Quercus ilex* and *Quercus faginea*), Spain (**a**). Underplanting of *Fagus sylvatica* in gaps of planted *Picea abies* stands, Slovenia (**b**). *Quercus robur* planted in groups with mounding site preparation and natural regeneration of *Betula* spp. between the groups, Sweden (**c**), and a mixture of planted *Fagus sylvatica* and naturally regenerated *Pinus sylvestris* protected from deer browsing by a 2.2-m-high fence (**d**). (Photos: Lluis Coll and Magnus Löf)

different oak species find appropriate conditions to germinate and establish underneath the more or less closed canopy of pinewoods spontaneously developed on abandoned agricultural land (Fig. 4.2a). Once the new species have established and reached a certain size, the relatively low light transmitted to the understory hampers their growth, and thus canopy openings of a certain extent are required for promoting them to more advanced developmental stages (Martín-Alcón et al. 2015).

In the absence of large disturbances, these openings may occur naturally (understory reinitiation stage), but their appearance can be accelerated through thinning treatments (Ammer 2017). The increased light reaching the soil in openings will not only favor the development of previously established species but of a range of other herbaceous and woody species (Gebhardt et al. 2014). Although in some cases the ground vegetation could interact positively with the desired regeneration (e.g., protecting the plants from browsing) (García et al. 2000; Jensen et al. 2012), in general it provides high competition to the seedlings (principally to those of lower size) compromising their survival and growth (Wagner et al. 2006). This is particularly true when grasses dominate the understory given their superficial and dense root systems and their high ability to extract water and nutrients from the soil (Coll et al. 2003, 2004). In the worst cases, some form of control of the ground layer is needed to ensure the success of the ongoing diversification processes at these stages of stand development (Balandier et al. 2006) (see also below).

When no seed sources of another tree species are present, creating mixed forests in pure stands could also be achieved by underplanting (i.e., enrichment plantations) or direct seeding beneath the canopy of pure stands (Paquette et al. 2006; Ammer et al. 2008; Martín-Alcón and Coll 2016) (Fig. 4.2b). When conducting such practices (see below in Sect. 4.4.2), particular care should be taken to select species that are able to tolerate shade and to control for potential negative effects due to belowground competition by the roots of the canopy trees (see, e.g., Ammer et al. 2002) or from ground vegetation (e.g., when the understory is dominated by shade-tolerant plants such as *Rubus* species or ferns (Balandier et al. 2013)). Finally, establishing mixtures during the stand reinitiation stage (by allowing natural regeneration of a range of species in the stand) or directly in gaps (by artificial planting and sowing) requires good knowledge of the growth habits of and the interactions between the species involved (Stanturf et al. 2014). In general, designing mixtures composed by species belonging to different functional groups (with different resource needs and abilities to capture and use them) may favor the occurrence of facilitation and complementary effects as the stands develop (Paquette and Messier 2013). For example, there can be facilitative effects in mixed stands composed by a N-fixing species and a non-N-fixing one (see, e.g., the classic experiments with Douglas fir and red alder reported in Binkley (2003)) and complementary effects due to denser canopy filling in mixtures compared to monocultures (Pretzsch 2014). However, these effects are known to vary spatially and temporally depending among other factors upon the quality of the sites, the climate, or the density of the stands (see reviews by Forrester 2014 or Forrester and Pretzsch 2015). This hampers the formulation of general rules about the type of mixture to establish or promote (in terms of composition, proportions, and pattern). In any case, an adequate control of ground vegetation is critical for successfully establishing mixtures by planting or seeding in open areas, particularly in fertile sites where grasses are dominant (Löf and Welander 2004; Picon-Cochard et al. 2006). In such conditions, as well as in areas with high browsing pressure or harsh environmental conditions (e.g., in the Mediterranean basin), direct and indirect facilitative effects by shrub species have been widely reported (Gómez-Aparicio et al. 2004; Kunstler et al. 2006; Jensen et al. 2012). Then, the use of shrubs as nurse plants could be envisaged (Castro et al. 2004; Gómez-Aparicio 2009).

4.4 Technical Aspects During Regeneration

4.4.1 Natural Regeneration

As mentioned earlier, natural regeneration with a mixed-species composition most often occurs in the stand initiating stage after major disturbances or at the understory initiation stage when mature forests start to open up their canopies (Fig. 4.1). Annual seed production, spatial seed distribution, and environmental conditions for germination and early growth of various tree species can cause large variation in regeneration success. Therefore, natural regeneration of mixed-species stands is less predictable compared to regeneration established through direct seeding or planting (see below). In the best case, the probability of obtaining natural regeneration of a mixture of species can be predicted using regeneration models or extrapolating from case studies. Even experiments with natural regeneration do not always develop as expected, and regeneration and ingrowth models are not working very reliably for single sites (Tremer 2008; Drössler et al. 2013). Therefore, the choice of such silvicultural methods requires sound ecological knowledge. Good practice includes the assessment of the forest site and the state of natural regeneration before harvest operations. Field surveys can be conducted to estimate regeneration density, spatial distribution, tree species proportions, height differentiation, area without sufficient regeneration and browsing damages, etc. (Raison et al. 2001). However, this work is often done manually at site and is labor intensive and costly. Many times it is also important to define a minimum seedling/sapling height for the various tree species. Overtopping and competition may result in high mortality as the regeneration develops. With a basic understanding of seed years, establishment, and growth pattern of various tree species under particular ecological conditions (light, soil moisture, nutrient supply, browsing pressure) and response to release cuttings, the potential for natural regeneration can be reasonably estimated. Leader lengths of advanced regeneration and regeneration in canopy gaps can provide additional information to estimate future height development of individual tree species (Petritan et al. 2007; Drössler et al. 2017). Generally, in regeneration of mixed-species stands compared to monocultures, more intensive tending is required to achieve a certain species proportion and especially to maintain less competitive tree species (Rumpf and Ditges 2008; Mason et al. 2018; Pach et al. 2018).

Mixtures of tree species often occur after larger canopy openings or following shelterwood cuttings (Gayer 1886; Karlsson 2001). Mechanical site preparation with the exposure of mineral soil can stimulate natural regeneration, especially on forest soils with a thick humus layer (Löf et al. 2012) (Fig. 4.2c). Obviously, this measure becomes more effective with increased seed supply (i.e., during mast years). There are different methods of mechanical site preparation, e.g., scarification or subsoiling, or mounding at wet sites. The effect on seedlings' number and their growth usually lasts for the first 2 years (until ground vegetation has recovered), but there are also negative effects on existing advanced regeneration with small seedlings removed or damaged since they are not visible for the machine operator. For some tree species (e.g., pine, birch, aspen), prescribed burning can be another measure to initiate dense regeneration (Vanha-Majamaa et al. 2007). In such mixed regenerations, the desired proportions of abundant tree species can be managed by pre-commercial thinnings, e.g., mixtures of Norway spruce and birch (Holmström et al. 2016a). Such interventions need to consider the tree species-specific growth dynamics and the faster growth of pioneer tree species at the beginning of the rotation but the decreasing growth rate in later years. The same applies to management of tree species mixtures consisting of planted and naturally regenerated seedlings, and it is often easier to manage group- than stem-wise mixtures (Saha et al. 2012; Holmström et al. 2016b). Rare tree species could also be promoted by selective release cuttings (or debarking) of their competing neighbors.

As mentioned earlier, mixed natural regenerations may also develop in the understory when the canopy starts to open up. After longer periods in such understories, shade-tolerant tree species will dominate the regeneration. For example, most shade-tolerant tree species in Europe will need at least 8–15% relative light to be able to establish and develop, while light-demanding tree species require at least 20–40% relative light (von Lüpke et al. 2004; Paquette et al. 2006; Ammer et al. 2008; Löf et al. 2007). Thus, in established mixtures of European beech (shade-tolerant) and Norway spruce (intermediate shade-tolerant), beech seedlings can be promoted by 20% removal of stocking volume in mature stands with dense canopy, while 40% removal promotes the development of spruce (as a rule of thumb) (Fig. 4.2b). However, such simple rules are lacking for many tree species combinations. It is important to manage such regeneration through several subsequent cuttings in the overstory. Besides manipulating the development of different tree species, this silvicultural regime also regulates the competing ground vegetation. Therefore, especially under extended periods between shelterwood cuttings where a continuous regeneration of late-successional tree species is expected, soil preparation measures may be omitted (Övergaard 2010; Drössler et al. 2017). If natural regeneration has only partially established in the stand and the mature trees need to be harvested, areas without seedlings can be replanted with other tree species (e.g., larch or Douglas fir to complement 5–20-year-old natural beech regeneration).

4.4.2 Direct Seeding and Planting

As outlined in the above sections, the establishment of mixed stands by natural regeneration requires a sufficient amount of seed trees and an efficient dispersal of the seeds. However, these two basic requirements are often missing. For example, in the stand initiation phase, after clear-cuts or on sites to be restored by afforestation, planting or direct seeding is required. The same is true in the understory reinitiation phase if a pure stand is to be converted into a mixed stand by establishing seedlings of one or more tree species below the shelter of the overstory trees (von Lüpke et al. 2004; Ammer et al. 2008). However, both techniques, direct seeding and planting, have advantages and limits, which will be briefly described below.

Direct seeding is a silvicultural measure where the seeds are placed directly on the site (Ceccon et al. 2016). It is considered to be less costly than planting (Palmerlee and Young 2010). Its main advantages apart from economy are (1) that poor planting practices and the often related poor root system development are avoided (Huth et al. 2017) and (2) that large areas can be covered using sowing machinery or horse-driven apparatuses. If successful, it provides (3) the option to yield wildlings, which can be used for plantings instead of seedlings from nurseries. Reforestation using direct seeding of Scots pine in northern Sweden and Finland and afforestation using direct seeding of oak are examples of successful regeneration using this method (Wennström 2001; Madsen and Löf 2005). Direct seeding may also be an inexpensive means of establishing mixtures through since often a more diverse mixture is established including naturally regenerated woody species when compared to planting (Twedt and Wilson 2002). However, disadvantages of direct seeding are the rather high uncertainty of germination, the low survival rates due to seed predation by various animals that may result in inadequate seedling density and/or distribution, and the long exposure of the seedlings to weed competition (e.g., Engel and Parrotta 2001; Grossnickle and Ivetic 2017). These drawbacks may counterbalance the initial low costs compared to plantings. To overcome the many problems related to direct seeding, a considerable amount of research has been carried out in the past two decades. Several studies have, for example, addressed seed quality (Wennström et al. 2002, 2007), pre-sowing seed treatment (Winsa and Bergsten 1994; Winsa and Sahlén 2001; Willoughby et al. 2004), the effect of soil type (Madsen and Löf 2005), different soil preparation techniques (Winsa and Bergsten 1994; Willoughby et al. 2004; Kankaanhuhta et al. 2009; Löf and Birkedal 2009; Birkedal et al. 2010), sowing depth (Birkedal et al. 2009), seed coverage (Nilson and Hjältén 2003), sowing date (Winsa and Sahlén 2001; Madsen and Löf 2005; Jinks et al. 2006; Birkedal et al. 2010; Hyppönen and Hallikainen 2011), overstory density (Ammer et al. 2002; Leder et al. 2003; Manso et al. 2013), weed control (Löf and Welander 2004; Willoughby et al. 2004; Jinks et al. 2006; Balandier et al. 2009), and the role of predators (Nilson and Hjältén 2003; Birkedal et al. 2010; Jinks et al. 2012). However, no general rules for successful direct seeding can be derived from these studies as tree species autecology and abiotic conditions differ strongly and there are no effective methods against seed predation available. In other words, direct seeding requires profound understanding of seed dormancy, seed predation, and soil and climate conditions favoring germination, supported by detailed knowledge of aligned sowing techniques (stratification, soil preparation, reduction of stand density, protection against rodents, weed control, etc.). Thus, much knowledge is still lacking.

Planting is much more frequently applied than direct seeding. Its main advantages are (1) to be largely independent from mast years, (2) to skip the vulnerable stage after germination, (3) to reduce interference from surrounding vegetation, and (4) to possibly design mixtures of any composition and distribution on the site. The latter is of special importance for the establishment of mixed stands. Disadvantages are the comparably high costs and the risk to negatively impact root development (Nörr 2003). Research has previously addressed many aspects of planting. This has resulted in a vast amount of literature referring to seedling quality (Rikala 2000) and stock type (Leugner et al. 2009; Jäärats et al. 2016); planting techniques (De Chantal et al. 2009; Luoranen and Viiri 2016); planting date (Palacios et al. 2009); root pruning (Andersen et al. 2000; Andersen 2001; Buraczyk and Kapuścińska 2010); supporting measures such as tube shelters (Puértolas et al. 2010; de Castro et al. 2014), nurse trees (Löf et al. 2014), soil preparation (Gemmel et al. 1996; Sahlén and Goulet 2002; Löf et al. 2006), and weed control (Hytönen and

Jylhä 2011; Jensen and Löf 2017); planting schemes and spatial arrangement (Saha et al. 2012; Collet et al. 2013; Andrzejczyk et al. 2015); and overstory density (Gemmel et al. 1996; Palacios et al. 2009). With regard to stock type, Grossnickle and El-Kassaby (2016) concluded in a recent review that "where plant competition is the main limiting site variable, larger sized bareroot and container stocktypes have the best chance for successful stand establishment." This finding may be of special importance for future plantings in a changing climate. Another topic, which should receive attention when establishing mixed stands, is the spatial arrangement of different tree species. Thus the different growth patterns of the species involved have to be taken into account. If, for example, a fast-growing species is planted next to a slow-growing tree species in a tree-by-tree mixture, frequent interventions to control the desired stand composition are very likely to be needed. In these cases, group mixtures are recommended to keep the different tree species apart from each other during the initial establishment phase (Krissl and Müller 1990; Saha et al. 2012) (Fig. 4.2c).

Relatively few studies have compared direct seeding and planting within the same study (Table 4.2). Basically they confirm that each method has its advantages and drawbacks and that the choice between them very much depends on the actual situation on site. If, for example, a competitive ground vegetation is already established and/or seed predators occur at high densities, direct seeding should not be the first choice. In other surroundings, however, direct seeding may be the preferred option, not least because of the low costs. For the establishment of mixed stands, a combination of both regeneration techniques may also be reasonable: it might be an option to plant a slow-growing tree species in a predefined pattern into a stand where another, fast-growing species has already been sown on a larger area. Another option for creating mixed stands by applying both techniques would be to use plantings to fill in gaps where directed seeding had failed. In conclusion, direct seeding and planting are important measures for the deliberate establishment of mixed stands, but their successful application requires profound knowledge of multiple aspects ranging from tree species ecology and soil science to technical issues and logistics.

4.4.3 Deer Management and Protection from Browsing

High deer populations in Europe and North America pose one of the greatest challenges to and impacts on the forest regeneration of many tree and herbaceous species, which further affects the species composition, forest structure, and function (e.g., Gill 1992; Ammer 1996; Rooney 2001; Weisberg and Bugmann 2003; Côté et al. 2004). Their selective browsing influences plant-plant interactions to an extent that browsing-tolerant or less palatable tree species often are favored (Kuijper et al. 2010). Royo et al. (2010) emphasize that ungulate impact is not just additive but complex and involves interactions and effects on other species groups as well as ecosystem nutrient cycling (Pastor and Cohen 1997). Finally, the release of deer

Table 4.2 Selected studies comparing the success of direct seeding and planting from boreal, temperate, and Mediterranean regions of Europe

Species	Region	Zone	Site	Attribute of interest	Results	References
Pinus sylvestris	Southern Finland	Boreal	Many sites of different soil moisture availability	Number of seedlings and height growth	Planting was the most effective method of regeneration on fresh sites and direct seeding on dryish and dry sites	Miina and Saksa (2008)
Quercus robur	Southernmost Finland	Hemiboreal	Regeneration sites	Survival and growth	Higher survival and better height growth of planted seedlings. Seedlings for direct seeding were approx 50% in height compared to planted seedlings (note: not corrected for age!). Direct seeding failed in 2 out of 8 stands	Valkonen (2008)
Fagus sylvatica	Southern Germany	Temperate	Shelter of mature *Picea abies* trees	Height growth, biomass production, and aboveground woody biomass allocation	Comparable height growth and aboveground biomass production per seedling if corrected for age. Lower share of branch biomass for sown seedlings than for planted seedlings due to higher density in the nearby neighborhood	Ammer and Mosandl (2007)
Quercus ilex	Southern Spain	Mediterranean	Former agricultural land	Survival, growth, and morphology	1-year-old planted seedlings of both species performed much better than sown seedlings and 3-year-old planted seedlings	González-Rodríguez et al. (2011)
Quercus suber						

populations from population control by natural predators combined with low-intensity hunting can foster shifts in the ecosystem functioning and create long-lasting legacy effects (Nuttle et al. 2014). The high deer populations therefore severely challenge silvicultural efforts to establish more species-rich forests by limiting the regeneration of a range of more palatable tree species. Additionally, several deer species find favorable habitats in modern landscapes. In many regions there is a mix of farm fields and varying amounts of forest cover from large forested landscapes to small woodlots and woody shelterbelts which is often combined with a total absence of predator populations. For example, in the managed forests, they find plenty of food during the stand initiation and in the understory reinitiation stages and good shelter in the stem exclusion stage (Fig. 4.1).

Deer impact can be reduced by either reducing the populations or increasing forest landscape carrying capacity for the deer or combining the two. Increasing the forest landscape carrying capacity is expected to reduce browsing pressure temporarily if the populations are allowed to expand. Since hunting and the associated revenue make deer important for both social (recreational) and economical (hunting) objectives in several countries, a significant reduction in deer populations is often controversial due to conflicting interests, or is not desirable for many forest owners. Physical or chemical protection of regenerations by deer fences, repellents, or individual protection (tree shelters, mesh, etc.) is usually efficient and important measures to protect seedlings of various tree species that are vulnerable to browsing by deer or other ungulates such as wild boar (*Sus scrofa*) (Fig. 4.2d). Unfortunately, the costs of establishing, maintaining, and removing these measures are usually high, while fences restrict access for deer to some of their most valuable habitats, which will increase deer pressure elsewhere in the forest landscape. The high costs are a major constraint to the extensive use of these protection measures for a widely implemented support for mixed-species regeneration unless government subsidies are available. Access to subsidies is, however, greatly dependent on national political priorities, and therefore such high-cost methods are unlikely to be relevant for wide-scale application in all countries.

Therefore, it is relevant to consider or implement an integrated management approach suggested by Rooney et al. (2015). The deer impact is potentially reduced by managing the forest landscape for increased deer carrying capacity and/or intensifies the culling to reduce or maintain a constant level of the deer populations. Rooney and coworkers recommend managing the forest landscapes according to six principles: (1) consider all elements of the system, (2) understand how management might change landscape carrying capacity, (3) incorporate landscape variability into measures of management success, (4) recognize non-forest food sources, (5) include social dimensions, and (6) integrate natural disturbance into restoration planning. Further, Rooney et al. (2015) highlight the importance of understanding and incorporating both historical and contemporary role of ungulates (deer) in the forests and landscapes.

Reimoser and Gossow (1996) demonstrated the potential of controlling or using the regeneration density as a key measure equivalent to improving the forest landscape carrying capacity, i.e., browsing risk was reduced in their studies with increasing density of seedlings in natural regeneration. Using natural regeneration or direct seeding for establishing mixtures can potentially provide densely stocked regeneration (e.g., 15–50,000 saplings/ha) at relatively low costs compared to planting. Regenerating mixtures of species by various combinations of natural regeneration, direct seeding, and/or planting offers ways of increasing deer carrying capacity while providing physical protection for the target species. These methods include using nurse trees planted in the same spot to protect the target species. Likewise, inter-planting target species under or near potential nurse trees or shrubs may provide more regeneration tolerant to deer browsing (Perea and Gil 2014). Typically, the nurse species is protecting the target species by providing physical protection. However, protecting plants may reduce browsing but will not serve as 100% protection (Jensen et al. 2012). To further increase carrying capacity, fodder crops, e.g., grasses, herbs, or woody species, may be established to release browsing pressure from forest regenerations or farm crops in the landscape. Supplementary feeding is also an option if the food source improves nutrition of the deer (Felton et al. 2016). The challenge is to transform the scientific findings into operational, site-adapted, and improved management systems that include both using more deer browse-tolerant regeneration methods and a clear strategy for the deer management in the context of sustainable and integrated forest landscape and game management. Research, development, and collaboration with practice to implement cost-effective methods and systems of this integrated approach are a key element in securing regeneration of the full range of woody species in mixtures.

4.5 Concluding Remarks

Mixed-species stands are more complex than monocultures, and this is true for all important ecological processes that determine seedling establishment and growth. Our paper have highlighted that this complexity requires more knowledge for any efficient management of mixtures. For example, only a few studies have addressed the specific seed production conditions in mixed forests. Distances between trees for pollen exchange can be much larger than in single-species stands which will influence seed production and frequency of fruiting years. The proportions of different tree species may also vary considerably between stands. Sometimes rare species only occur in small numbers or as single trees, which may result in large variations in seed densities that may be below minimum densities for seed production. Thus, here we need more information. In addition, we have little knowledge about seed predation from various animals in mixed stands compared to pure ones.

However, in general larger tree crowns produce more seeds. Thus, from a manager's perspective, it is important to reduce crown competition in the species that is favored in the present stand, as well as to create conditions for the regeneration of future stands. Such management uses thinning operations and requires knowledge of the species-specific shade tolerance and growth dynamics in relation to other tree species. In Europe and for the most common tree species, such information is available. At the same time, for many less common tree species, such basic information is still lacking, and more research is needed.

Due to their complexity, mixed-species regenerations are less predictable compared with regenerations of monocultures. This makes it complicated to formulate general rules for development and requires more knowledge compared to monocultures for management. Any management action taken to create a mixture needs to consider the competitive ability of the species involved and the expected outcomes of their interactions, which may vary in time and space. When evaluating different options for creating management guidelines, one way forward may be to gather different tree species in different functional groups, i.e., light demanding, intermediate shade tolerant, and shade tolerant, and manage according to this even though complete knowledge of the traits for all species is not available. One starting point from a management perspective is to estimate the development potential of different tree species in newly established mixed natural regeneration. Simple field surveys can be conducted to estimate density, spatial distribution, proportions, height differentiation, area without regeneration, and browsing damages. To evaluate development potential, the competitive status (dominant, overtopped, etc.) is important to define a minimum height for the various tree species. Leader shoot lengths of seedlings can provide additional information about their growth potential. This type of information is often relatively expensive to gather in the field. Here new techniques such as drone remote sensing for forestry applications are becoming increasingly appealing. The current methods are still at an experimental stage, but it would be very helpful if low-cost high-resolution systems with small drones as platforms for surveying, measuring, and distinguishing different tree species in potential young mixed forests could be developed.

Compared with monocultures, more management interventions are required in mixed-species stands to maintain the desired proportions of different tree species and especially to maintain the less competitive tree species. Simultaneously and in the absence of large disturbances, openings of the canopy layer may occur naturally (understory reinitiation stage), but their appearance could be accelerated through thinning treatments. As a consequence of thinning, more light will reach the forest floor. For managers, it is important to balance the amount of light so that any new regeneration can establish and develop but at the same time prevent the establishment of extensive ground vegetation. Such herbaceous and grass vegetation may outcompete tree seedlings if not controlled. In the worst cases, some form of control of the ground layer is needed to ensure the success of the ongoing diversification processes at these stages of stand development.

The choice of regeneration method depends largely on the starting point and aim of the regeneration. If seed trees of suitable tree species are present in the vicinity of the regeneration site, natural regeneration should be considered. Natural regeneration also provides the possibility to create dense regeneration that may tolerate browsing (see below) and normally results in lower costs compared to artificial methods. Otherwise, direct seeding or planting has to be used. Artificial regeneration is also needed if the management objective is to change plant material for, e.g., productivity reasons, changing tree species or adapt management to climate change.

Direct seeding is a low-cost alternative to planting with the possibility of creating dense regeneration. However, and especially during reforestation, the success of direct seeding is generally less predictable than planting. Tree species differences in seed dormancy, optimal germination conditions, and susceptibility to seed predation are obstacles for successful seeding of mixed-species stands. In these fields we need more basic knowledge. In addition, there is often a variable supply of seeds. Therefore, direct seeding requires profound knowledge from managers, and for several tree species, we have too little knowledge to be able to give practical recommendations for direct seeding. Planting is more costly but also more predictable. Throughout the development of a young plantation, our study has highlighted that it is often easier to manage group- than stem-wise mixtures. This is important information for practice since it also opens possibilities for planting fewer seedlings, thus reducing costs, and may require new guidelines if both planting (groups) and natural regeneration (between groups) are used simultaneously. However, for many tree species combinations, we need more information about optimal design of such group plantations (distance between groups and seedlings, amount of seedlings, etc.). There is also a need of more information on how to effectively establish transplants of different tree species to be used in such combinations. Most research to date on seedling establishment has been carried out on only a few tree species, but different tree species respond differently to measures such as vegetation control, mechanical site preparation, and release treatments in young stands.

We have also highlighted that high deer populations are perhaps the greatest challenge for regenerating mixtures. Their selective browsing often creates an apparent competitive situation where less common tree species are damaged whereas some competitors are not. This may affect the whole tree species composition and biodiversity in the landscape. Hunting is an effective tool for reducing deer populations, but hunters are often interested in maintaining high populations for recreation and economic reasons, and, thus, there is sometimes a major conflict between hunting groups and forest owners interested in more diverse forests. There are several management tools to be used for protecting individual seedlings and mixed regenerations (e.g., fencing, other physical protections, and repellents). The may be effective, but a common feature is that regeneration costs often increase to a level where state subsidies are needed for any implementation. Therefore it seems to be wiser to try to develop strategies that manage both deer populations and their food across the landscape, in other words, to develop methods that keep populations at lower levels simultaneously as any browsing effects are diluted and not concentrated in the landscape. However, this will require much more information and knowledge and greater cooperation between researchers and different stakeholder groups for efficient implementation at larger scales.

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Chapter 5
Growth and Structure in Mixed-Species Stands Compared with Monocultures: Review and Perspectives

Hans Pretzsch

Abstract Forest structure, growth, and yield determine many ecosystem functions such as wood production, carbon sequestration, and landscape aesthetics. Mixed stands are on the advance as they can provide many ecological and social ecosystem functions and services better than monospecific stands. This chapter gives a brief overview of the current knowledge of tree species mixing effects on growth at the stand, species, and tree level.

First, results from experimental plot and inventory data will be used for showing the effect of tree species mixing on stand productivity and other stand characteristics such as mean stand height and diameter, tree number, stand basal area, and standing volume, growth, and yield per unit area. Second, long-term experiments provide insight into the effect of mixing on tree size distribution and spatial stand structure. Third, mixing effects are traced to the tree level regarding shape, allometry, and growth of individual trees in mixed versus monospecific stands. Fourth, a brief overview is given regarding the main causes why growth and yield of mixed-species stands often differ from monocultures and how mixing effects depend on the particular species assemblage, the prevailing environmental conditions, and the stand structure. Fifth, the focus will be on the transition from the analysis to the design of mixed-species stands and how to remedy knowledge gaps.

5.1 Stand Growth and Yield

The reason for the increasing attention given to mixed-species stands is that close-to-nature approaches, which often involve the use of mixed-species stands, are widely held to supply ecological, economic, and sociocultural forest goods and services at a similar or higher level than many monocultures (Bauhus et al. 2017a; Hooper et al.

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2005; Hector and Bagchi 2007). However, sound knowledge about mixing effects, even for the most common tree species combinations, is rather rare and scattered. Just in the last few years, after the failure of some monocultures and rethinking on risk distribution (Knoke et al. 2005), resource efficiency (Richards et al. 2010), and the functional significance of species diversity (Scherer-Lorenzen et al. 2005), mixed stand dynamics have become a focus of forest science (see, e.g. Scherer-Lorenzen et al. 2005; Pretzsch et al. 2010, Forrester et al.2006).

In this section we give an overview of the relative productivity of mixed-species stands compared with monocultures. Following the concept introduced by del Río et al. (2018), the productivity of the mixed stand is compared with the weighted mean productivity of neighbouring pure stands of the same species. A mixed stand productivity equal to the weighted mean productivity of the monocultures would indicate a simple additive effect. A productivity above or below (over- or underyielding, respectively) the weighted mean would mean a multiplicative mixing effect, which is of special scientific interest because it indicates beneficial or detrimental interspecific interactions. A mixed stand productivity even greater than the productivity of the most productive monoculture (transgressive overyielding) is of special interest for decision-making in forest practice. The next section considers both over- or underyielding and transgressive overyielding or degressive underyielding. For further details of calculating over- and underyielding, see del Río et al. (2018).

5.1.1 Overview Based on Long-Term Experiments

Knowledge on the advantages or disadvantages of mixed versus monospecific stands, with respect to productivity, decisively influences the forest owners' decisions in favour or against mixed-species stands (Olsthoorn et al. 1999). Figure 5.1 shows the results of a recently compiled meta-analysis on stand productivity of mixed and pure stands based on long-term experiments of common species combinations in Germany (Pretzsch and Forrester 2017). It revealed a mean overyielding of 19% for Norway spruce (*Picea abies* (L.) KARST.) and European beech (*Fagus sylvatica* L.) (Fig. 5.1a) and 24% for sessile oak (*Quercus petraea* (MATT.) LIEBL.) and European beech (Fig. 5.1b) which is in line with other studies mainly based on mixtures of two species (Piotto 2007; Zhang et al. 2012).

Figure 5.1c shows a 20% overyielding for the species combination of Norway spruce, silver fir (*Abies alba* MILL.), and European beech. Latter three-species mixture is very common in the mountainous areas of Europe (Alps, Carpathians). The meta-analysis of results, based on 46 plots in Alps, showed that the mean relative productivity amounted to 120% of the neighbouring monocultures, while the absolute gain in productivity amounted, on average, to 1.60 t ha^{-1} $year^{-1}$. A similar evaluation for two experiments with six plots and three-species mixtures of sessile oak, European beech, and Scots pine (*Pinus sylvestris* L.) in the hill country of Steigerwald and Spessart also yielded, on average, a higher productivity in

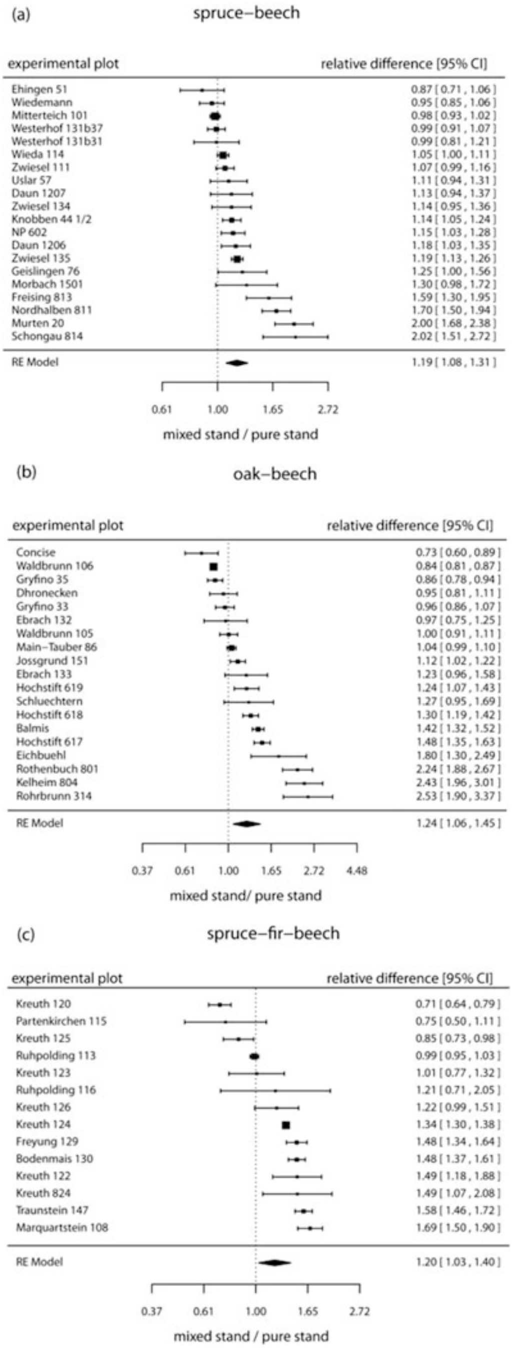

Fig. 5.1 Comparison of the stand productivity of mixed versus monospecific forest stands based on long-term experimental plots in Central Europe (**a**) Norway spruce (*Picea abies* (L.) KARST.) and European beech (*Fagus sylvatica* L.), (**b**) sessile oak (*Quercus petraea* (MATT.) LIEBL.) and European beech, (**c**) mixed mountain forests of Norway spruce, silver fir (*Abies alba* MILL.), and European beech. On average, the mixed stands produced 119%, 124%, and 120%, respectively, of the weighted mean of the neighbouring monocultures. All three analyses revealed a broad variation in mixing effects including underyielding and strong overyielding (After Pretzsch and Forrester 2017). The entry "Wiedemann" in (**a**) refers to the results of the study by Wiedemann (1942) about the growth of mixed versus monospecific stands of Norway spruce and European beech

mixtures than in monocultures (amounting to 143%) and an absolute productivity gain of 1.89 t ha^{-1} $year^{-1}$. Although based on a rather small database, these results are indicative given the scarce information available to date on the effect of three-species mixtures. The size of the mixing responses (on average 120–143% in relation to the neighbouring monocultures) stresses that in three-species mixtures, the absolute gain as well as the variation can be even higher than in two-species mixtures (Fig. 5.1c), consistent with many studies that have examined the relationships between tree species richness and growth (Forrester and Bauhus 2016; Liang et al. 2016; Pretzsch et al. 2013b).

The ultimate data sources for assessing the performance of mixed versus monospecific stands at a given site are long-term records of the total yield covering the whole rotation period. However, with the exception of short-term rotation plantations, such records are extremely rare. Therefore, most mixed-species stand analyses are based on growth records from single- or short-term surveys. The longer the growth period covered by the survey, the more the results from growth-based evaluations converge to total yield-based findings. As a result of mixing effects changing with age, insight into long-term mixing effects requires either long-term survey over longer periods or sampling of stands at different ages (real or artificial time series). However, sampling should also cover different time spans in terms of calendar years because mixing effects can also vary depending on periodic environmental conditions. Restriction of the analysis to a limited time span may produce biased results when environmental conditions during the measurement period have been above or below the average. Sound findings require sampling over a broad range of stand ages and calendar years and surveys over a broad range of site conditions.

Analysis of over- and underyielding on long-term experiments reaching over nearly the whole rotation for mixtures of sessile oak and European beech and Norway spruce and European beech showed that the overyielding in terms of total yield can exceed the results of short-term-based analysis (Pretzsch and Forrester 2017). The yield-based evaluation reflected higher benefits from mixture (1.06 and 1.14, resp.) compared with evaluations over short-term periods with a low performance in mixed compared with pure stands.

5.1.2 Overview Based on Inventory Data

The still rather fragmentary knowledge of mixing effects on forest stand productivity has been complemented by analyses of forest inventory data (del Río and Sterba 2009; Gamfeldt et al. 2013; Vallet and Perot 2011; Vilà et al. 2013). Compared with the restricted number of long-term mixed-species experiments, forest inventories represent mixing effects for a much broader range of site conditions, species assemblages, stand ages, mixing proportions, mixing patterns, and stand densities (Condés et al. 2013; Forrester and Pretzsch 2015; Toïgo et al. 2015). But in contrast to the ceteris paribus conditions and causal evidence of mixing effects on experimental plots (Pretzsch et al. 2010, 2013a), inventory data analyses only provide the statistical relationship between species composition and productivity, e.g. an overyielding of mixed in comparison to monospecific stands may result from a predominance of mixed stands on slightly better sites compared with monocultures. A complete disentanglement of the species composition-productivity relationship from all confounding co-variables is rarely possible using inventory data because information about, e.g., stand history, site conditions, thinning, and mortality, is often simply lacking in the case of forest inventory data. Thus, inventory data analyses may substantiate but not replace mixed-species stands analyses based on experimental data (Nagel et al. 2012).

Using forest inventory data at the regional or national level, several studies found that overyielding of mixed versus pure stands was modified by site conditions (Toïgo et al. 2015), stand density (Condés et al. 2013), and various other stand characteristics (Vilà et al. 2013). In contrast to stand productivity, dominant stand height was hardly affected by tree species mixing (Vallet and Perot 2016). Liang et al. (2016) quantified the effect of tree species richness on the productivity of many of the world's forested ecosystems in the most comprehensive study so far. They used repeated forest inventories from 777,126 permanent sample plots that contain over 30 million trees representing 8737 tree species and span most of the global terrestrial biomes. They found a consistently positive concave-down relationship between stand productivity and tree species richness at landscape, country, ecoregion, and global levels (Fig. 5.2). Globally, a 10% loss of tree species richness corresponded on average to a 6–7% decline in productivity, and the rate of this decline increased significantly with a further reduction of biodiversity. This relationship revealed that continued biodiversity loss at landscape scales would result in an accelerating decline in forest productivity worldwide. The relationship between tree species richness and stand productivity was strikingly similar across global climates and biomes despite some geographic variation. The study by Liang et al. (2016) highlighted both the negative effect of biodiversity loss on forest productivity and the potential benefits from the transition of monocultures to mixed-species stands in forestry practices. The relationship between tree species richness and productivity that they discovered across forest ecosystems worldwide corresponded well with experimental and observational studies on forest and non-forest ecosystems.

5.1.3 Synthesis of Facts on Overyielding of Mixed Versus Pure Stands

The overyielding of mixed versus monospecific stands revealed in this section is clearly of a magnitude that is worthwhile exploring further and tracing from the stand to the tree and organ levels. Table 5.1 summarises the overyielding of common two-species assemblages in Central Europe and underlines the fact that the mixing

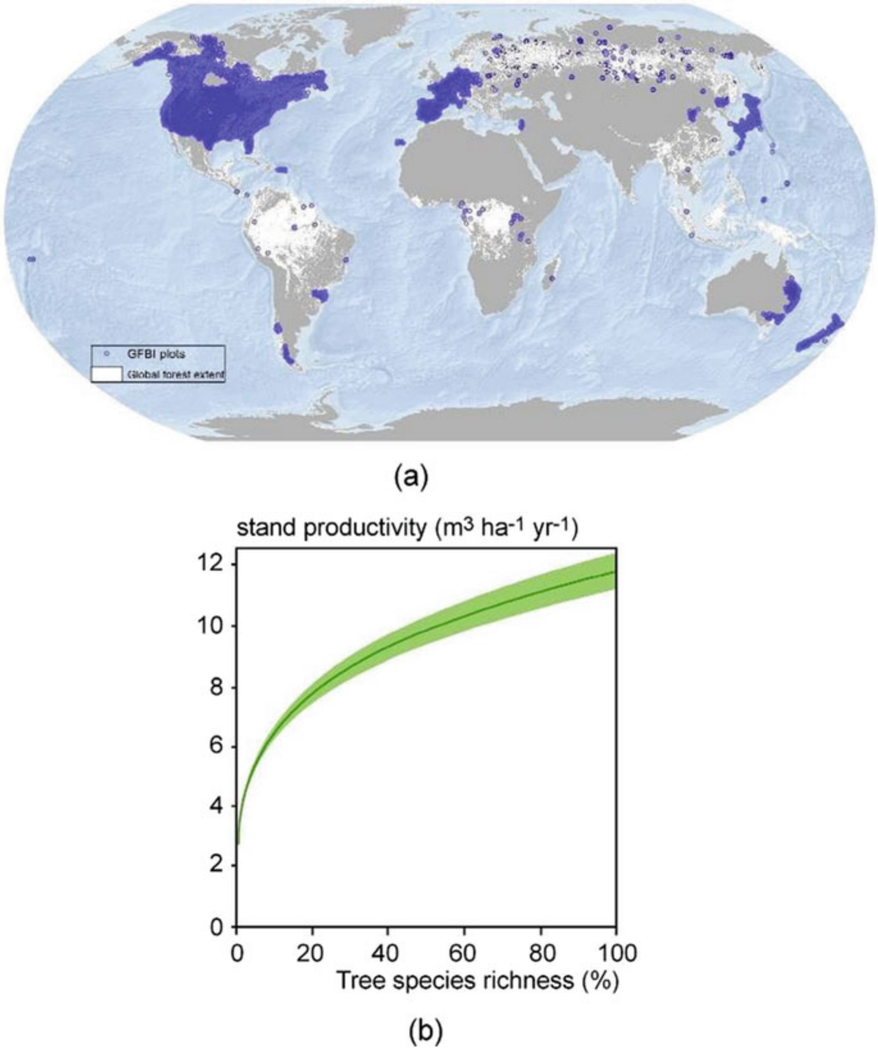

Fig. 5.2 Global effect of tree species richness on forest productivity according to Liang et al. (2016). Analysis of data from 777,126 global permanent sample plots reflected by grey dots in (**a**) revealed a consistent positive and concave-down tree species richness-productivity relationship (**b**) (After Liang et al. 2016)

effects are not only scientifically evident but also practically relevant. Long-term experiments show that in relation to the weighted mean of the monospecific stands, mixed-species stands produce 11–30% more stem volume (Pretzsch 2016). Combinations of less complementary species (e.g. Norway spruce and European beech, Norway spruce and silver fir) result in lower overyielding than complementary species combinations (e.g. Scots pine and European beech, European larch (*Larix*

Table 5.1 Mixing effects on stand productivity of various tree species mixtures in Central European forests derived from long-term experiments according to Pretzsch and Forrester (2017)

Species combination	N. sp./E. be	S. pi/E. be	s. oak/E. be	E. be/D-fir	S. pi/N. sp	E. la/N. sp	N. sp./s. fir	Mean
Overyielding	21	30	20	11	21	25	13	
(±SE) in %	(±3)	(±9)	(±3)	(±8)	(±11)	(±6)	(±6)	
Corr. factor	1.10	1.20	1.10	1.10	1.20	1.20	1.10	1.10

The relative overyielding (%) refers to the productivity of the mixed-species stands in relation to the weighted mean of the neighbouring monospecific stands (for calculating the relative productivity of mixed versus pure stands, see del Río et al. 2018). The correction factors may be used to conservatively adjust the stand productivity of monospecific stands to the expected stand productivity of the respective species assemblages (Pretzsch 2016)

N. sp. Norway spruce (*Picea abies* (L.) Karst.), *E. be.* European beech (*Fagus sylvatica* L.), *S. pi.* Scots pine (*Pinus sylvestris* L.), *s. oak* sessile oak (*Quercus petraea* (Matt.) Liebl.), *D-fir* Douglas-fir (Pseudotsuga menziesii Mirb.), *E. la.* European larch (*Larix decidua* Mill.), *s. fir* silver fir (*Abies alba* Mill.)

decidua MILL.) and European beech). In addition to the mean overyielding and standard error, Table 5.1 shows conservative correction factors which may be used to estimate mixed stand productivity based on the productivity of neighbouring monocultures. The correction factors indicate that the productivity of monocultures should be multiplied by 1.10–1.20 to estimate the productivity of the respective mixed-species stands, and they apply for fully stocked mixed-species stands, individual to groupwise mixing patterns and mixing proportions of about 50:50.

The correction factors may serve as a makeshift for deriving mixed-species stands productivity from neighbouring pure stands as long as more accurate model approaches for predicting mixing effects are missing (Fabrika et al. 2018). Any application of the correction factors should consider that mixing effects on productivity may be modified by stand structure and site conditions (see Sect. 5.5.2). The correction factors in Table 5.1 are mainly based on works on Norway spruce and European beech by Kennel (1965), Pretzsch et al. (2010), and Rothe (1997), on Scots pine and European beech by Pretzsch et al. (2015a), on sessile oak and European beech by Pretzsch et al. (2013a), on European beech and Douglas fir by Thurm and Pretzsch (2016), on Scots pine and Norway spruce by Wellhausen et al. (2017), on European larch and Norway spruce by Zöhrer (1969), and on Norway spruce and silver fir by Pretzsch et al. (2013b).

5.1.4 Considerations of the Productivity Gains by Tree Species Mixing

Overyielding up to 50% reported by Caspersen and Pacala (2001), Hector et al. (1999), and Pfisterer and Schmid (2002) for grasslands can hardly be transferred to managed forests in Central Europe. Presumably, in temperate forests of Central Europe, niche differentiation is comparatively low due to species reduction in the course of the ice ages and due to the much slower evolutionary and co-evolutionary processes of long-lived trees. This may be a reason why the plus of productivity of mixed stands compared with pure stands is much lower in long-lived forest than in short-lived herbaceous stands. Many of the European forest stands are "artefacts" designed with very productive species such as Norway spruce and Douglas fir cultivated outside their natural habitats. Often, genetic variation in these species no longer reflects natural selection but a choice controlled by human's commercial criteria. These forests are therefore not designed for optimum niche utilisation by the mixture species. Compared with overyielding found in the subtropics and tropics and for atmospheric nitrogen-fixing tree species (DeBell et al. 1989; Forrester et al. 2006, 2007; Kelty 1992), the reported mixture effects of about 10–30% for commercial tree species in temperate and boreal zones appear rather moderate.

In comparison with annual systems, the lifespan of forests is longer at two orders of magnitude and the danger from risks consequently much greater. In addition cyclic disturbances through silvicultural treatment also take their toll. It is for this reason that the risk distribution in forests achieved in mixtures carries so much more weight than in short-lived ecosystems. Unfortunately, most yield comparisons between pure and mixed stands usually refer to more or less undisturbed stands. Affected plots are abandoned after calamities or unplanned use, and only undisturbed plots are kept under continuous observation. Statements about inferiority or superiority derived from these experiments therefore also apply merely to "normal" circumstances. If response patterns after disturbances were also considered, yield comparisons would become more realistic. According to that the productivity relationship between pure and mixed stands under "normal" conditions may shift considerably once risks are included (Pretzsch 2003). The decisive factor here, in essence, is the probability of the occurrence of disturbances and damage. Thus, beyond the potential of direct increase or decrease of productivity, species mixing may indirectly change productivity by risk distribution and resilience and can alter a broad set of other forest functions and services (Hector and Bagchi 2007; Pretzsch 2005; Scherer-Lorenzen et al. 2005).

Most studies quantify the mixing effects on productivity based on stand basal area or stem volume growth. The results may change when effects of mixing on the crown, the branch fraction, the root-shoot allometry, or the wood density would be taken into consideration (see Sects. 5.4.2 and 5.4.3). However, assessment of the total above- and below-ground biomass is much more challenging in forest compared with grassland systems.

5.2 Yield Components at the Mean Tree and Stand Level

Most of the studies introduced in the previous section quantify overyielding of mixed-species stands versus monocultures of 10–30% but hardly consider other scientifically or practically relevant stand characteristics beyond stand productivity (del Río et al. 2016). In this section yield components at the mean tree and stand level such as mean tree characteristics, stand density measures, and stand volume and yield characteristics will be used for comparing mixed-species stands with monocultures introduced by del Río et al. (2018).

5.2.1 Effect of Mixing on Mean Tree Size, Tree Number, and Standing Stock

Based on 141 combinations of mixed stand plots and neighbouring monocultures of common tree species mixtures in Central Europe, Pretzsch et al. (2016a) and Pretzsch and Biber (2016) showed the effect of mixing on yield components at the mean tree and stand level. They analysed long-term experimental plots and temporary plots in Central Europe in even-aged mixed stands and monocultures of silver

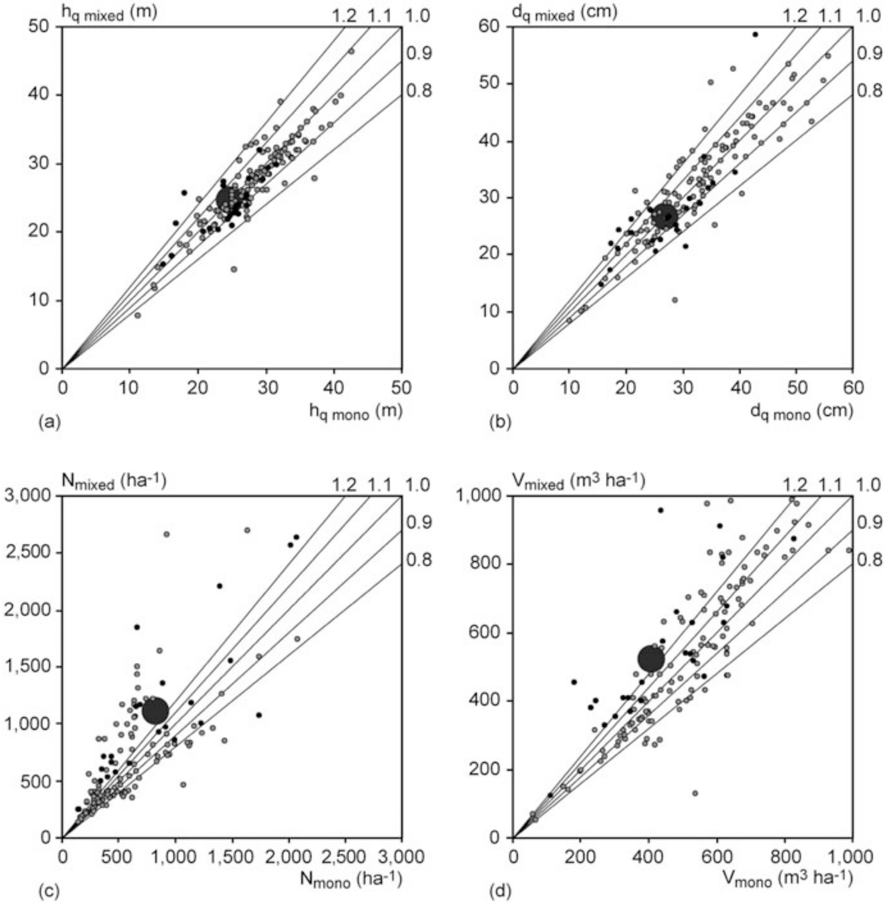

Fig. 5.3 Mean tree height (**a**) and quadratic mean tree diameter (**b**) in mixed-species stands are on average rather similar to the respective mean tree dimensions in the neighbouring monocultures. Tree number (**c**) and standing volume (**d**) are on average higher in mixed-species stands compared with neighbouring monocultures. Small dots represent the results of individual experiments; large dots represent mean values. Values near the bisector line (1.0 line) indicate similar levels in mixed-species stands and monocultures regarding the stand density and standing stock. (After Pretzsch et al. 2016a)

fir/Norway spruce, Norway spruce/Scots pine, Norway spruce/European larch, Norway spruce/European beech, Norway spruce/black alder (*Alnus glutinosa* (L.) Gaertn.), Scots pine/European beech, European larch/European beech, European beech/sessile oak, and European beech/Douglas fir that represent maximum stand density.

The mean stand height (−2%) and tree diameter (+1%) of mixed stands hardly differ from the weighted mean values of the neighbouring monocultures (Fig. 5.3). Minor inferiorities in the mean dimension of one species are mostly compensated by

Table 5.2 Species mixing can significantly increase the stand density and standing stock but leaves the mean tree values almost unchanged compared with neighbouring monocultures

Variables	Units	Sample sizes	Group means (± SE)		Ratios
		n	Mixed	Mono	Mixed/mono (±SE)
Mean tree dimensions					
h_q	m	141	29.25 (± 0.52)	29.85 (± 0.50)	0.98* (± 0.008)
d_q	cm	141	32.10 (± 0.88)	32.18 (± 0.85)	1.01 (± 0.100)
v_q	m^3	141	1.36 (± 0.09)	1.37 (± 0.09)	1.05 (± 0.033)
Stand density and standing volume					
N	Trees ha^{-1}	141	752 (± 54)	635 (± 40)	1.22*** (± 0.040)
BA	m^2 ha^{-1}	141	42.12 (± 1.43)	38.09 (± 1.12)	1.12** (± 0.024)
SDI	Trees ha^{-1}	141	793 (± 27)	717 (± 20)	1.16*** (± 0.025)
V	m^3 ha^{-1}	141	561.38 (± 21.66)	525.59 (± 19.52)	1.08** (± 0.026)
Total stand volume yield					
TY	m^3 ha^{-1}	79	979.85 (± 42.50)	883.85 (± 37.61)	1.12** (± 0.027)
Eichhorn's rule and general yield level					
V_{h20}	m^3 ha^{-1}	141	325.57 (± 13.06)	282.06 (± 8.40)	1.16** (± 0.028)
TY_{h20}	m^3 ha^{-1}	79	509.42 (± 21.59)	419.78 (± 13.13)	1.21*** (± 0.030)

Species mixing can significantly increase the stand density and standing stock but leaves the mean tree values almost unchanged compared with neighbouring monocultures. The table displays the stand characteristics for mixed-species stands in Central Europe (group mean for mixtures) in relation to the weighted mean of neighbouring monocultures (group mean for monocultures) and ratios mixed/mono. Ratios above/below 1.00 indicate a superiority/inferiority of the species' performance in mixed-species stands versus monocultures. Ratios in bold numbers indicate significant differences ($p < 0.05$) between mixed-species stands and monocultures (after Pretzsch et al. 2016a)

The mean of the ratios (mixed/mono) is not necessarily equal to the ratio of the means (mean mixed/mean mono). So, we report both the groupwise arithmetic means (mean mixed and mean mono) and the mean ratios of the pairwise comparison (mixed/mono). The mean ratios of the pairwise comparison (mixed/mono) were used for testing group differences

Mean of the tree height, diameter, and individual tree volume, d_q, h_q, v_q; tree number per hectare, *N* stand density index by Reineke (1933), *SDI* standing stock of volume, *V* total yield, *TY* standing volume at index stand height 20 m, V_{hq20} total yield at index stand height 20 m, TY_{hq20}

a minor superiority of the other species (Table 5.2). The stand density, indicated by the tree number, the stand density index, the stand basal area, and the standing volume, in contrast, are 8–22% higher in mixed stands compared with monocultures (Fig. 5.3, Table 5.2). In most mixtures both species increase their stand density compared with the neighbouring monocultures.

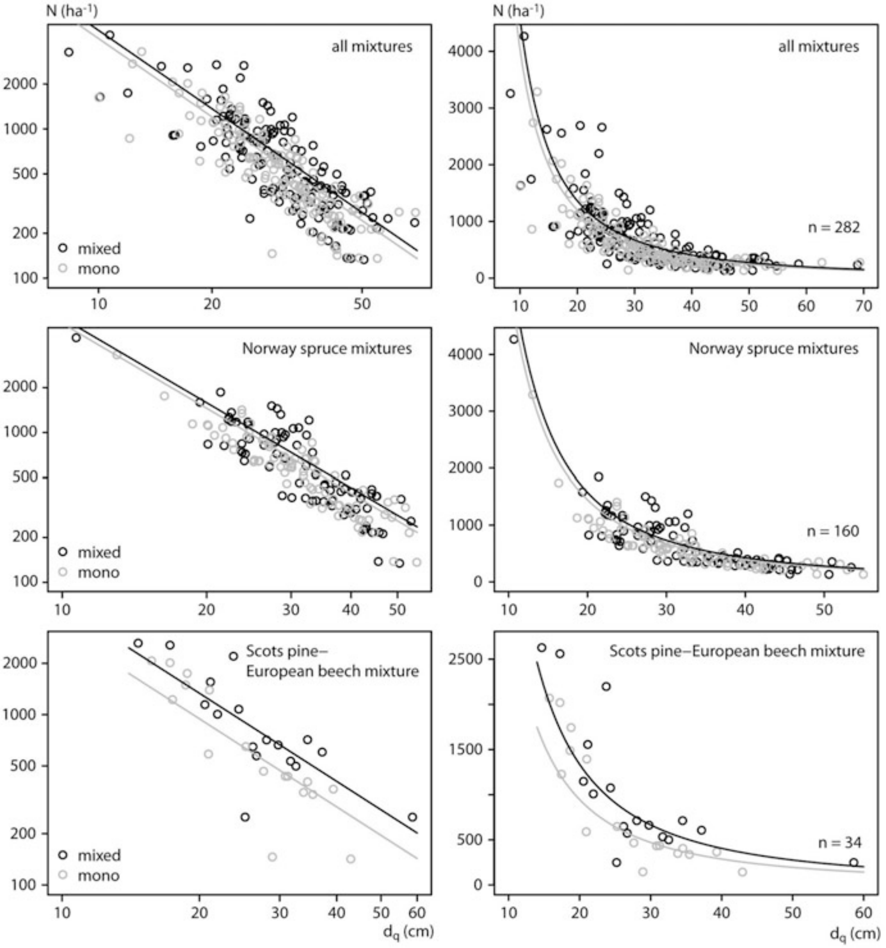

Fig. 5.4 Increase of the maximum stand density by tree species mixing indicated by an upward shift of the relationship between tree number per hectare and mean tree diameter in double-logarithmic (left) and linear (right) representation. For all species assemblages, the self-thinning line of the mixed stands (black lines) lies above the weighted mean self-thinning line of the two monocultures (grey lines). (Data from Pretzsch and Biber 2016)

5.2.2 Stand Density Index and Self-Thinning Line

Based on triplets of fully stocked and unthinned long-term plots of mixed-species stands and neighbouring monocultures, Pretzsch and Biber (2016) revealed over-density of mixed-species stands on the basis of the mean diameter-tree number relationship in double-logarithmic (left) and linear (right) representation (Fig. 5.4). Most mixtures included Norway spruce. The evaluation showed that in mixed stands

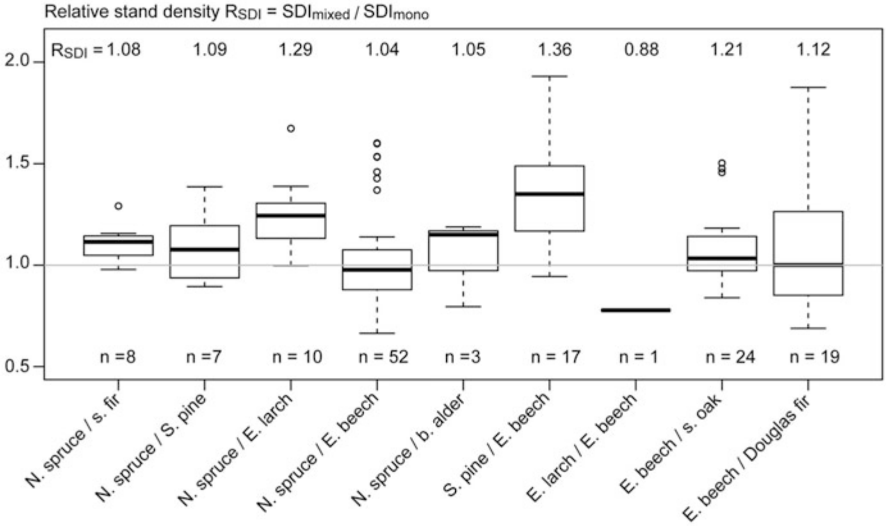

Fig. 5.5 Boxplots of the relative stand density (SDImixed/SDImono) for various species assemblages according to Pretzsch and Biber (2016). Numbers above the boxes indicate the relative stand density (SDImixed/SDImono). In the cases of spruce-larch and pine-beech, the deviations of the relative stand density from the density of the monoculture (RSDI = 1.0) were significant

maximum density was on average 16.5% higher than in neighbouring pure stands. Species mixtures with Norway spruce exceeded densities of monospecific stands by 8.8% on average. Individual species mixtures showed a significant density effect of +29.1% for Norway spruce mixed with European larch and +35.9% for Scots pine in association with European beech. The self-thinning line of all the mixed stands (black) lay above the weighted mean self-thinning line of the two monocultures (grey). The level of the self-thinning was raised by species mixing, whereas the slope remained the same. This shows that mixing can reduce tree mortality of the total stand so that their self-thinning line can be significantly higher (Bravo-Oviedo et al. 2018; Ducey et al. 2017).

The mixing effect on stand density can also be analysed for each single species assemblage separately (Pretzsch and Biber 2016). Except for larch-beech, where there was only one observation available, the relative stand density (SDImixed/SDImono) was always higher than 1.0 and varied between 1.04 and 1.36. In the cases of spruce-larch and pine-beech, it is significantly so with mixture-induced density gains of about 29% and 36% (see Fig. 5.5). Both significant effects are observed in species associated with a highly shade-tolerant species (European beech) or an intermediately shade-tolerant species (Norway spruce) mixed with a very light-demanding species (European larch, Scots pine). Note that any shifts in the self-thinning line mean a change of the mortality process in mixed-species stands compared to monocultures.

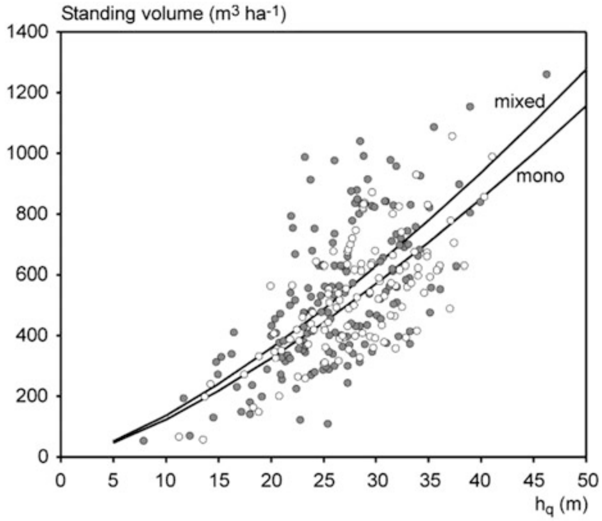

Fig. 5.6 Standing volume, V, over stand mean height, h_q, for monoculture (empty symbols) compared with mixed-species stands (filled symbols). Regression analysis revealed a significant increase of the rule by Eichhorn (1902) in mixed compared to monospecific forest stands. (Pretzsch et al. 2016a)

5.2.3 *Effects of Mixing on the Yield Level*

The rule by Eichhorn (1902) describes the relationship between stand volume and mean height (V = f(h)), whereas the general yield level by Gehrhardt (1923) and Assmann (1961, pp. 158–160) describes the relationship between total yield and mean tree height (TY = f(h)). The following analysis of how tree species mixing affects total yield and the yield level (Eichhorn 1902; Assmann 1961) was based on the 141 combinations of mixed stand plots and neighbouring monocultures mentioned at the beginning of this section (see Pretzsch et al. 2016a).

Comparison between the standing volume, V, and total yield, TY, of mixed and monospecific stands can be based on general allometric relationships which allow the extrapolation of V and TY to an index stand height of 20 m (Pretzsch and Biber 2016). This allows the comparison of Eichhorn's rule and the general yield level in mixed-species stands versus monocultures even when the underlying long-term experiments differ in terms of the stand development phase. The combination of rather invariable mean height and increases in stand density and total yield results in a significant increase in the level of the relationship by Eichhorn (+16%) and the general yield level by Assmann (1961) (+21%) in mixed versus pure stands (Fig. 5.6, Table 5.2).

Mixing modified stand density, standing volume, and total yield rather than tree height and site index (Pretzsch et al. 2016a; Vallet and Perot 2016). The increase in stand density, Eichhorn's rule, and general yield level should be taken into consideration when modelling stand growth (e.g. modification of self-thinning slopes and mortality modules developed for monocultures), inventory of standing volume by yield tables (e.g. correction of yield table estimates by the measured degree of stocking), or development and application of silvicultural prescriptions in mixed-species stands (e.g. increased normal density and number of selected future crop trees).

Whereas findings in mixed-species stands versus monocultures have been consistent for these central European species (e.g. Vallet and Perot 2016), further empirical investigations would be necessary to provide evidence of these patterns for different species assemblages.

5.3 Size-Structure Dynamics

In the following there will be applied several measures and indices for characterizing the 3D stand structure, tree size distribution, and canopy space occupation in mixed-species stands and comparing them with monocultures. For calculation of these and other measures and indices, see Pretzsch et al. (2016a), Pretzsch (2017a) and del Río et al. (2018).

5.3.1 Mixing Effect on the Tree Size Frequency Distribution

In many temperate forests, trees compete strongly above ground for light. As a result of this competition for light, tree size distribution, growth partitioning between the trees, and canopy density of mixed-species stands can change fundamentally and may contribute to an overyielding compared with neighbouring monocultures.

Figure 5.7 is a schematic representation of the effect of mixing on the tree size distribution according to Pretzsch and Schütze (2016). Their analysis was based on 42 triplets in monospecific and mixed stands of Norway spruce/European beech, Scots pine/European beech, Douglas fir/European beech, and Norway spruce/Scots pine. Each triplet consists of three plots with two in monospecific stands and one in a mixed stand of the respective species. Only those species which play a major role in forestry in both monospecific and mixed-species stands were included in the analysis. All included plots represent more or less even-aged and monolayered forest stands. The plots have not been recently thinned and represent high to maximum stand density. Mixed plots should represent individual tree mixture and a mixing proportion of about 50:50.

Figure 5.7 shows that the total number of trees can be higher in mixed stands compared with monocultures. In addition, the minimum tree size can be smaller and the maximum size larger. The skewness and the kurtosis can also be higher. The higher tree number and lower minimum tree size results mainly from shade-tolerant species like beech which had reduced growth but can survive below more light-demanding and transparent species such as pine. The alien-thinning can proceed less rigorously than the self-thinning, especially in the case of beech, which has the

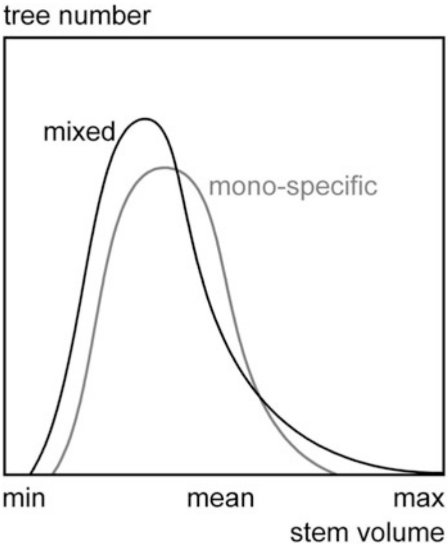

Fig. 5.7 Characteristic size distribution of mixed stands compared with monocultures. The minimum tree sizes in mixed stands were lower, and the maximum tree sizes were higher, but the mean size was rather similar compared with monocultures. In mixed stands, the tree numbers were higher and the size distributions more left steep (skewness >> 0) and more peaked (kurtosis >> 0). In contrast, the size distributions in monocultures were more symmetrical and flatter. (Pretzsch and Schütze 2016)

lowest self-tolerance of the species investigated (Pretzsch 2006; Zeide 1985). Trees of the species with superior size can accelerate growth and grow ahead. Due to its size superiority, this species can slow down the other species so that the latter lags behind and takes on a more subdominant position. This explains the higher maximum tree size and wide range of sizes in mixed stands compared with monocultures also found by Buongiorno et al. (1994) and Coomes and Allen (2007).

5.3.2 *Mixing Effect on the Inequality of Size and Growth Partitioning*

A series of 42 triplets with 126 plots of pure and mixed stands of Norway spruce/European beech, Scots pine/European beech, Douglas fir/European beech, and Norway spruce/Scots pine was used for analysing the inequality of size and growth partitioning (Pretzsch and Schütze 2016). The Gini coefficients GC_v in Table 5.3 (upper section) indicate that the inequality is mostly significantly higher in mixed-species stands compared with monocultures (GCv mixed/GCv mono = 0.95–2.09). Figure 5.8a, b illustrates this general tendency. It shows the cumulative stem volume as a function of the cumulative tree count for all monocultures and mixed-species stands of the triplets. The mean curves (bold lines) indicate that the smallest 50% of the trees account for 25% of the total stand volume in monocultures and for just 15% in the mixed-species stands. This inequality in size indicates a high number of small trees and a restricted number of tall trees in mixed stands. In monocultures, in contrast, the trees are more equally sized.

Table 5.3 Gini coefficients for volume, GC_v, and Gini coefficients for volume growth, GC_{iv} (mean ± standard deviation), in mixed-species stands versus monocultures (from top to bottom)

Species	***n***	**GC_v for volume**			**GC_v mixed/GC_v mono1**				**GC_v mixed/GC_v mono2**			
1/2		**Mean mixed**	**Mean mono 1**	**Mean mono 2**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**
N. sp./E.be.	11	0.41 ± 0.02	0.30 ± 0.03	0.44 ± 0.03	0.91	2.24	1.47**	0.14	0.63	1.33	0.95	0.06
Sc. p./E.be.	7	0.37 ± 0.02	0.32 ± 0.04	0.39 ± 0.04	0.83	2.64	1.74**	0.27	0.73	1.44	0.98	0.09
D.-fir/E.be.	18	0.54 ± 0.02	0.38 ± 0.02	0.42±0.03	0.64	3.37	1.79***	0.18	0.96	3.21	1.38**	0.12
N. sp./Sc. p.	6	0.47 ± 0.02	0.31 ± 0.03	0.23±0.02	0.71	1.84	1.29	0.17	1.50	2.81	2.09***	0.18
Species	***n***	**GC_{iv} for volume growth**			**GC_{iv} mixed/GC_{iv} mono1**				**GC_{iv} mixed/GC_{iv} mono2**			
1/2		**Mean mixed**	**Mean mono 1**	**Mean mono 2**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**
N. sp./E.be.	11	0.42 ± 0.02	0.35 ± 0.03	0.47 ± 0.03	0.78	1.69	1.24**	0.08	0.72	1.28	0.92	0.05
Sc. p./E.be.	7	0.40 ± 0.02	0.29 ± 0.05	0.45 ± 0.05	0.78	2.39	1.66*	0.27	0.71	1.33	0.96	0.10
D.-fir/E.be.	18	0.59 ± 0.02	0.39 ± 0.03	0.45 ± 0.03	0.72	2.54	1.64***	0.12	0.95	2.90	1.41***	0.10
N. sp./Sc. p.	6	0.49 ± 0.01	0.41 ± 0.04	0.28 ± 0.02	0.80	1.83	1.27	0.15	1.39	2.31	1.83***	0.18

Coefficients of GC_v and GC_{iv} close to 0.0 indicate equality of size and growth, respectively. Coefficients close to 1.0 indicate high inequality in size or size growth (after Pretzsch and Schütze 2016)

Note that in the columns “Mean mixed”, “Mean mono 1”, and “Mean mono 2”, we report the arithmetic means of all n observations within the respective groups. In the columns “Mean mixed/mono 1” and “Mean mixed/mono 2” in contrast, we report the mean of the ratio resulting from the pairwise division of the characteristic of the mixed-species stands by the respective value of the neighbouring monocultures. “*”, “**”, and “***” indicate significant differences between mixed-species stands and monocultures at the level $p < 0.05$, 0.01, and 0.001

N. sp. Norway spruce (*Picea abies* (L.) KARST.), *E. be.* European beech (*Fagus sylvatica* L.), *S. pi.* Scots pine (*Pinus sylvestris* L.), *D.-fir* Douglas fir (Pseudotsuga menziesii MIRB.)

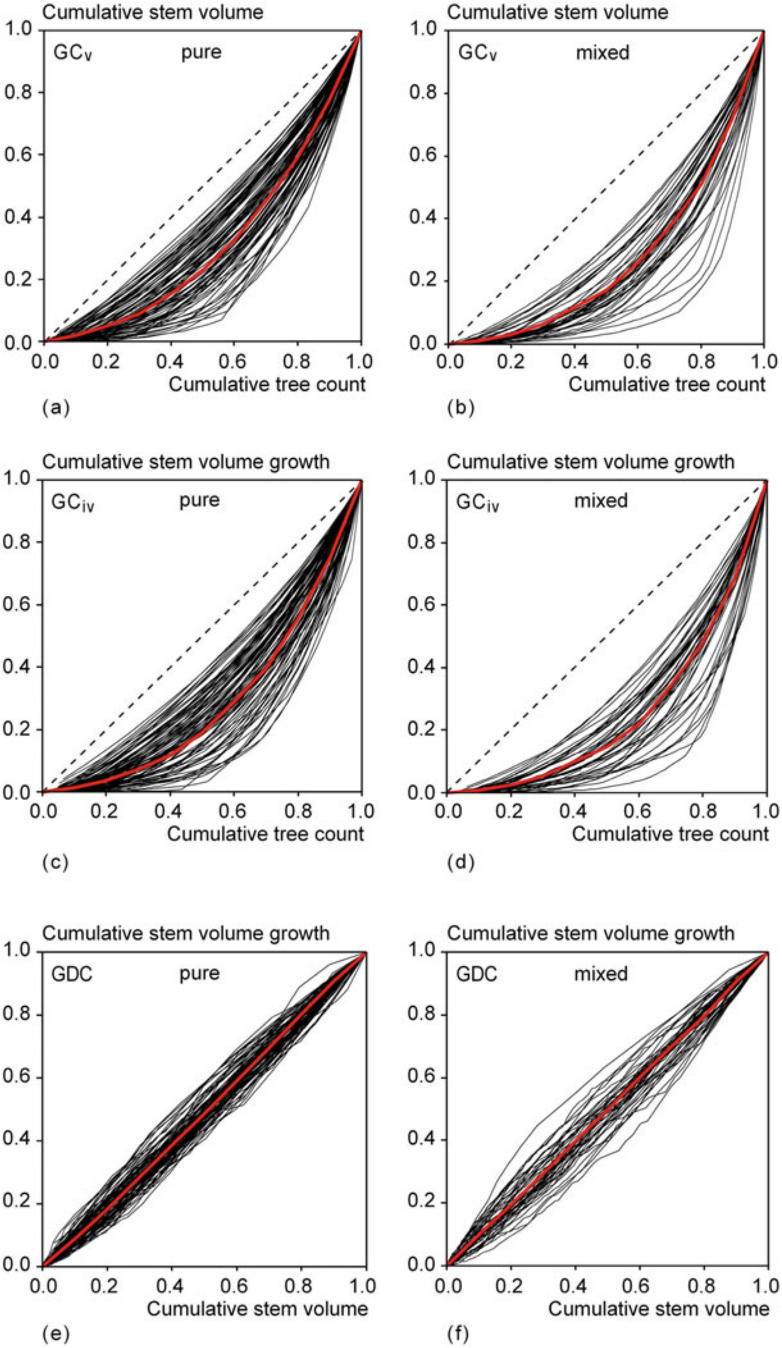

Fig. 5.8 (**a**–**f**) Hierarchy of tree volume, stem volume growth, and growth dominance for 84 monocultures (**a**, **c**, **e**) and 42 mixed stands (**b**, **d**, **f**) of the triplet series of Norway spruce/European beech, Scots pine/European beech, Douglas fir/European beech, and Norway spruce/Scots pine (After

The finding of higher inequality in mixed-species stands versus monocultures also applies for the growth partitioning among the trees within the stands, represented by GC_{iv} (Table 5.3, lower section). This is illustrated by the cumulative stem volume growth as a function of the cumulative tree count in Fig. 5.8c, d. That both GC_v and GC_{iv} are mostly significantly higher in mixed-species stands than in monocultures indicates a more unequal size distribution and growth partitioning in mixed stands.

In contrast, the growth dominance coefficients (GDCs) (Binkley et al. 2006) show only small and non-significant absolute differences between mixed and monospecific stands (Fig. 5.8e, f). The coefficient, GDC, is the cumulative stem volume growth, iv, as a function of cumulative stem volume, v, and results from GC_{iv}-GC_v. The GDC lies close to the 1:1 line (GDC = 0). The ratios between GDCs in mixed versus monospecific stands vary strongly but do not differ significantly from GDC = 1.0.

5.3.3 Remarkable Growth-Structure Elasticity of Mixed-Species Stands

Both GC_v and GC_{iv} indicate a much more unequal partitioning of stem volume and stem volume growth among the trees in mixed compared with monospecific stands (Fig. 5.8a–d, Table 5.3). Mixed stands have many small trees on the one hand and a strong concentration of volume and growth on a restricted number of tall trees on the other hand. Monocultures have greater equality of size and growth distribution. Table 5.3 showed that the difference between GC_v and GC_{iv} is rather similar for monospecific (on average $GDC = GC_{iv}\text{-}GC_v = 0.40\text{–}0.36 = 0.04$) and mixed stands (on average $GDC = GC_{iv} - GC_v = 0.50\text{–}0.46 = 0.04$). So, the coefficients of growth dominance ($GDC = GC_{iv} - GC_v$) are also similar and near GDC = 0 (varying closely around the 1:1 line in Fig. 5.8e, f) for monospecific and mixed stands. As the stem volume growth partitioning is very similar to the stem volume partitioning, the relationship between cumulative growth and cumulative volume is rather proportional.

Fig. 5.8 (continued) Pretzsch and Schütze 2016). (**a** and **b**) Cumulative stem volume, v, as a function of the cumulative tree count, n. On average, the Gini coefficients for monocultures ($GC_v = 0.36 \pm 0.01$) are significantly lower than for neighbouring mixed stands ($GC_v = 0.46 \pm 0.01$) of the same species. (**c** and **d**) Cumulative stem volume growth, iv, as a function of the cumulative tree count, n. On average, the Gini coefficients for monocultures ($GC_{iv} = 0.40 \pm 0.01$) are significantly lower than for neighbouring mixed stands ($GC_{iv} = 0.50 \pm 0.02$) of the same species. (**e** and **f**) Growth dominance coefficient, GDC, which is the cumulative stem volume growth, iv, as a function of cumulative stem volume, v, and results from GC_{iv}-GC_v. On average, GDCs of monocultures (GDC=0.02±0.01) are not different to those of mixed-species stands (GDC=0.01±0.01)

This reveals a remarkable growth elasticity of mixed-species stands. The reasons for this constant GDC, even under strongly varying stand structure, are probably the complementary ecological traits in mixed stands. A combination of light-demanding species in the upper canopy and shade-tolerant species in the lower canopy ensures that the relative contribution of the stem growth of small trees does not stay behind their portion of stem volume.

Mixing may release the competitive pressure in mixed stands through niche complementarity and thus result in a proportional relationship between cumulative growth and cumulative volume – although density, inequality, and size asymmetry are much higher than in monocultures. Species mixing seems to equalise the relationship between cumulative growth and cumulative volume and thereby guarantee a continuously low-growth dominance and size-proportional contribution of all trees to the stand growth.

5.3.4 Canopy Space Filling in Mixed Versus Monospecific Stands

For closer analysis of the canopy space filling, Pretzsch (2014) used 253 crown maps in monocultures ($n = 87$), 2-species ($n = 111$), and $\geq$3-species ($n = 55$) mixed stands in Germany. All three groups comprise even-aged and uneven-aged stands of mainly Norway spruce, European beech, sessile and common oak, Scots pine, silver fir, and sycamore maple (*Acer pseudoplatanus* L.). The following analysis of the canopy space filling in mixed versus monospecific stands is based on combined measurement of tree positions and crown sizes (crown length and crown projection area) on long-term experimental plots. The crown measurements ($n = 35{,}728$ measured crowns) date back to the 1950s and cover a broad range of tree species growing in monospecific and mixed stands. For a detailed account of eight-radii-crown measurements, see Pretzsch (2009, pp. 115–118). The stands have a mean plot size of 0.30 ha and stand ages of 16–283 years. From plots with repeated crown surveys, we included only those with $\geq$10 years between the successive inventories in order to avoid autocorrelation between the measurements.

The 95% and 75% percentile regression lines in Fig. 5.9a show that the sum of crown area amounts to 150% and 100%, respectively, in monospecific stands and increases with species richness by up to 220% and 180% (95% and 75% percentile). That means that in the fully stocked mixed stands, tree species are so densely interlocked that the sum of the crown projection area can become more than twice the stand area. The relationship between ground coverage by crowns and tree species richness shown in Fig. 5.9b demonstrates that in most fully stocked mono- as well as polycultures, 5–10% of the stand area is uncovered by crowns. The frequently reported mechanical abrasion (Putz et al. 1984) resulting in crown shyness may cause the 5–10% uncovered area in both monospecific and mixed stands. The wide variation in ground coverage below the ceiling line (95% and 75% quantile

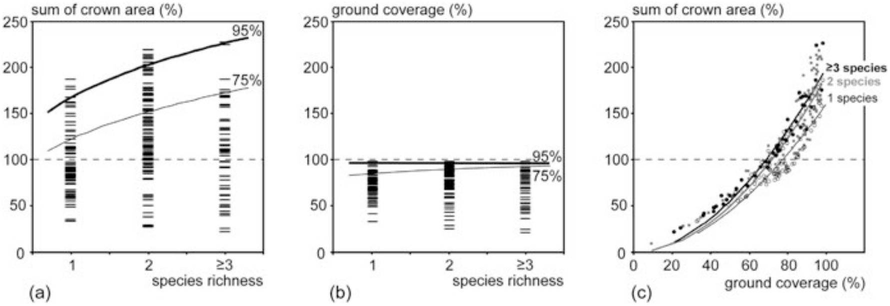

Fig. 5.9 (**a**–**c**) Sum of crown projection area per unit area and ground coverage in mixed compared with monospecific stands according to Pretzsch (2014). (**a**) Sum of crown projection area per unit area depending on tree species richness, (**b**) ground coverage depending on tree species richness, and (**c**) sum of crown projection area per unit area depending on ground coverage and tree species richness. Data are 253 crown maps of 187 plots belonging to 52 long-term experiments in even-aged and uneven-aged stands in Germany with mean plot size 0.29 ha, earliest and latest survey from 1951 and 2004, minimum and maximum stand age of 16 and 283 years, respectively. The 95% and 75% quantile regression lines in **a**, **b** represent the sum of crown area and ground coverage for fully and loosely stocked stands. The OLS regression lines in **c** represent the mean sum of crown area per unit area depending on ground coverage for ≥3-, 2-, and 1-species stands (upper, middle, lower line, respectively)

regression lines) can be attributed to the broad range of thinning grades included in the dataset of 253 crown maps. The above finding that species richness may increase the sum of the crown projection area even when the ground coverage is similar becomes even clearer in Fig. 5.9c. Especially in denser stands with ground coverage of >80%, the sum of crown projection area per unit area is about 25% higher in three-species stands compared with monocultures (upper versus lower line in Fig. 5.9c).

Studies in mixed-species stands by Kennel (1965), Pretzsch (2009, pp. 267–269), and Preuhsler (1981) suggest that the sum of crown projection area per unit area is often much higher than the ground coverage due to an up to sevenfold crown overlap especially in polycultures of species with complementary ecology. When studies comparing crown coverage between stands only count once areas which have been covered twice or more often, they neglect that the sum of the crown areas and all related advantages such as structural heterogeneity, growth, and resilience may be underestimated (Assmann 1970, pp. 102–107).

Based on long-term experimental plots in Germany in monospecific and mixed stands of spruce and beech ($n = 110$) as well as oak and beech ($n = 74$), the phenomenon of multiple crown coverage is analysed more closely (see Table 5.4). The crown measurements cover the period from 1954 till the present and stand ages of between 26 and 207 years. In order to study species-specific behaviour in coping with crowding, only fully stocked and rather even-aged stands were included, in which all species were left unthinned or were only moderately thinned.

Table 5.4 shows that the ground coverage by crowns is on average only 64–83% in monocultures and 85–88% in mixture; i.e. in both kinds of stands, a considerable portion is uncovered by crown projection area. Of special interest is that about

Table 5.4 Ground cover by crowns (mean ± standard error) in even-aged monocultures and mixed stands of Norway spruce (*Picea abies* (L.) Karst.), European beech (*Fagus sylvatica* L.), and sessile oak (*Quercus petraea* (Matt.) Liebl.) based on crown maps of unthinned and moderately thinned stands

	Stand		Ground	Ground	Onefold and multiple ground coverage			
			Cover	Uncovered	Onefold	Twofold	≥Threefold	Rel. sum of crown area
Species	Type	*n*	(%)	(%)	(%)	(%)	(%)	(%)
Norway spruce	Mono	32	77 ± 2	23 ± 2	64 ± 1	12 ± 2	1 ± 1	91 ± 4
European beech	Mono	25	83 ± 3	17 ± 3	50 ± 2	26 ± 3	7 ± 1	123 ± 7
N. sp. and E. be.	Mixed	53	88 ± 1	12 ± 1	48 ± 2	30 ± 1	10 ± 1	138 ± 4
Sessile oak	Mono	22	64 ± 4	36 ± 4	50 ± 2	12 ± 3	2 ± 1	81 ± 7
European beech	Mono	25	83 ± 3	17 ± 3	50 ± 2	26 ± 3	7 ± 1	123 ± 7
S. oak and E. be.	Mixed	27	85 ± 3	15 ± 3	35 ± 2	30 ± 2	20 ± 3	156 ± 10

The uncovered and covered stand area adds up to 100%. In addition, columns 5–8 give the percentage of onefold, twofold, and ≥ threefold crown cover and the relative sum of crown projection areas (Pretzsch 2014)

40–50% of the mixed stand ground area is covered more than onefold with crown projection area. The respective range in monocultures is 13–33%. The more multiple coverage in mixed versus monospecific stands is also reflected by a relative sum of crown area of 138–156% in mixed stands compared with 81–123% in monocultures. Even in monocultures, beech achieves 83% crown cover with 33% more than onefold coverage, indicating its outstanding shade tolerance and crown plasticity.

Comparing monocultures and mixed stands reveals the "overpacking" of the canopy space in mixed stands compared with neighbouring monocultures. The term overpacking is used as an analogy with overyielding, which refers to the frequently observed superiority of mixed stands regarding productivity. Particularly species combinations with complementary light ecology such as Norway spruce and European beech as well as sessile oak and European beech may lead to much denser and vertically layered canopies which in turn may cause higher light interception (Jucker et al. 2015; Kelty 1992; Morin et al. 2011) and overyielding (Bauhus et al. 2004; Pretzsch et al. 2010, 2013b) compared with monocultures.

5.4 Individual Tree Structure

This section focuses on the structure of individual trees growing in inter- versus intraspecific environments. The individual tree is exposed to and responds to the prevailing environmental conditions. The properties of the individuals determine the forest stand dynamics as individuals of different species interact with each other. Therefore, the level of the individual tree is most suitable for understanding competition, competition reduction through complementarity, and facilitation. Many of the beneficial tree mixing reactions result from complementary crown and root shape or modification of growth allocation and allometry introduced in this section.

Because of the complementarity in crown shape (e.g. a combination of ⍰-shaped [top heavy] with ▲-shaped [bottom heavy] crowns shown in Fig. 5.10) and resource demand (e.g. combination of light-demanding and shade-tolerant species), tree crowns may denser occupy the canopy space and expand more widely in inter- compared with intraspecific environments (Metz et al. 2013). On top of that, mixing can change the crown expansion such as crown radius and length and the inner crown properties such as branch length, branch angle, number of branches, and their straightness (Bayer et al. 2013; Bayer and Pretzsch 2017).

5.4.1 Shift in Crown Allometry in Interspecific Compared with Intraspecific Environments

Tree species mixing can considerably reduce a tree's competition and increase its lateral crown expansion even when the stand density in mixture equals that in

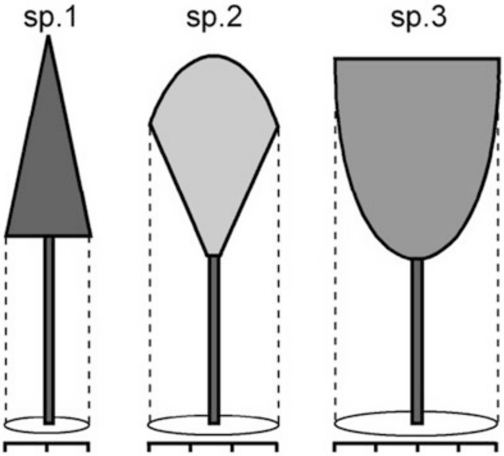

Fig. 5.10 Tree crown shapes can resemble slim cones (sp. 1), opened umbrellas (sp. 2), or very wide bowls (sp. 3) (After Pretzsch 2017b). Correspondingly, their crown radius, crown diameter, and projection area can vary considerably, and their packing density in mixed compared with pure stands may be higher (see also Fig. 5.12)

monoculture (Dieler and Pretzsch 2013; Jucker et al. 2015). Of special relevance for stand dynamics, growing area efficiency and stand productivity are the behaviour of the lateral and vertical crown extension in mixed versus monospecific stands. This determinates both a tree's growth and its space occupation and competition pressure on its neighbours.

We use data from Bavarian long-term experiments in monospecific and mixed stands of Norway spruce and European beech (Pretzsch and Schütze 2009) to scrutinise any shift in morphology caused by intra- versus interspecific competition. Figure 5.11 shows that the lateral and vertical crown extension of (a) Norway spruce and (b) European beech is higher in mixed than in monospecific stands.

Scaling between cpa and d is shallower in mixed than in monospecific stands but lies at a higher level in mixture (Fig. 5.11a). With increasing size, the collectives become more similar in this regard, i.e. in young and middle-aged stands, the species profit from interspecific competition but in mature stands, where crowns are less restricted, crown extensions become similar. The intercepts of the allometric relationships in mixed stands differ considerably from those in monospecific stands; crowns are significantly longer in mixed compared with monospecific stands. The h-d allometry, in contrast, is only slightly modified by species mixing. Note that by comparing the species' behaviour based on their scaling, size differences are eliminated.

Analysis of cpa-d allometry of beech in monocultures compared with beech in mixture with Norway spruce, European larch, common ash (*Fraxinus excelsior* L.), sessile oak, and Scots pine shows striking differences (Fig. 5.12). This analysis is based on densely stocked stands with no or only light thinning. Mixing matters even when the stand density is at maximum. Obviously a neighbouring European beech restricts the crown of a beech more than any other of the analysed species. For a beech with stem diameter 25 cm, the allometric equation shown in Fig. 5.12 (be) predicts a crown projection area of cpa = 17 m^2. Beeches with the same stem diameter achieve up to cpa = 45 m^2 when mixed with spruce, larch ash, oak, or

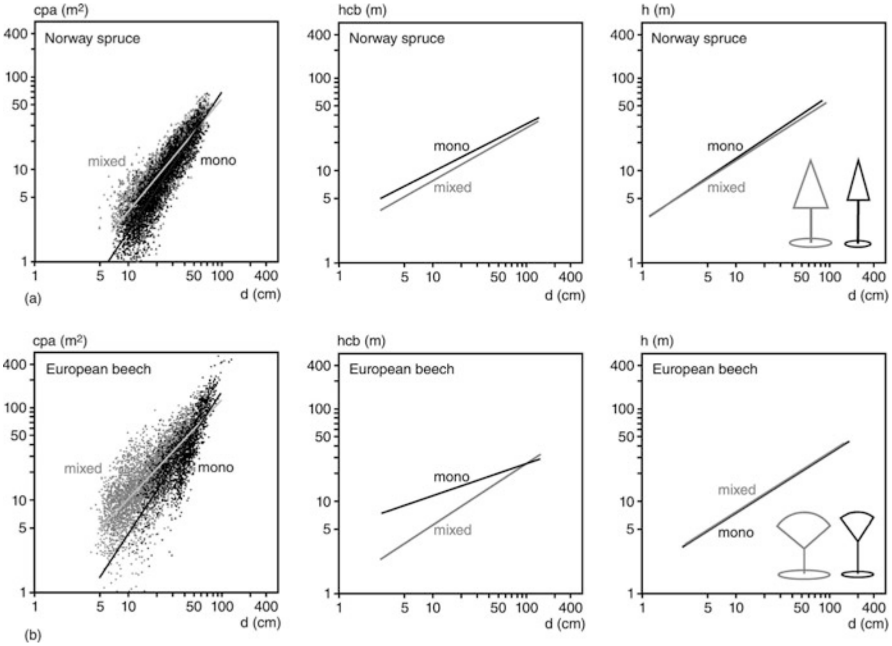

Fig. 5.11 Crown allometry of (**a**) Norway spruce (*Picea abies* (L.) KARST.) and (**b**) European beech (*Fagus sylvatica* L.) in mixed stands (grey) compared with monospecific stands (black). Mixing significantly increases lateral and vertical crown extension in terms of the relationship between crown projection area, cpa, and tree diameter, d, and between height to crown base, hcb, and tree diameter, d. It hardly changes the relationship between tree height, h, and tree diameter, d. (After Pretzsch 2014)

pines. The ranking of neighbours regarding the effect on crown restriction is beech > ash > spruce > larch > oak > pine. For European beech, mixing with each of the other species means "competition reduction" in terms of crown extension in the sense of Kelty (1992) and Vandermeer (1992). In other words, a neighbouring Norway spruce, sessile oak, or Scots pine means a relief in crown restriction compared with a neighbouring beech. This is in accordance with findings by Pretzsch and Biber (2005) that self-thinning is the highest in beech monocultures and much lower in stand of the other tree species.

Solitary trees achieve wide and, apart from a slight tendency towards ovality due to one-sided solar irradiation in northern or southern latitudes, rather circular crowns. The symmetry of their crowns indicates unimpeded lateral expansion or at least all-round homogeneous restriction by, for example, water, light, or nutrients (Møller and Swaddle 1997). When coping with crowding, crowns may adapt their lateral extension to their prevailing neighbourhood conditions and increasingly lose the symmetry typical for solitary growth. Species with higher crown plasticity can to some extent overcome their restriction by occupying emerging niches, penetrating neighbouring crowns, or even edging out neighbours.

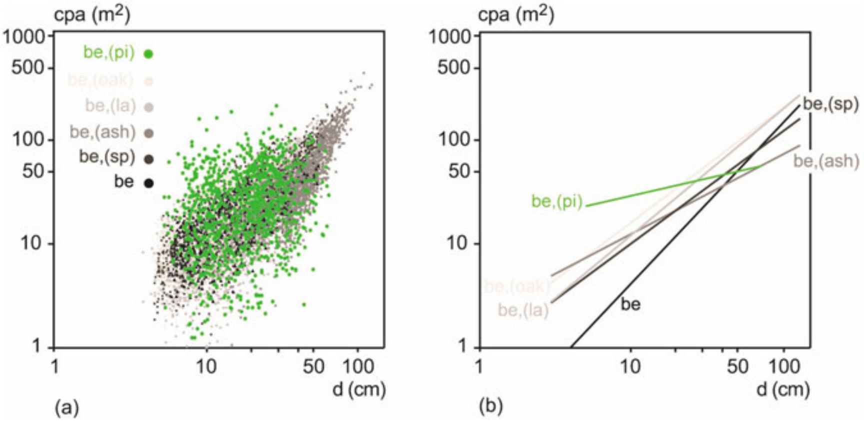

Fig. 5.12 Allometric relationship between crown projection area, cpa, and the tree diameter, d, for European beech (*Fagus sylvatica* L.) in monocultures (black) and shift in the allometry when beech is mixed with Norway spruce (*Picea abies* (L.) Karst.), European larch (*Larix decidua* Mill.), common ash (*Fraxinus excelsior* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and Scots pine (*Pinus sylvestris* L.). (Modified after Pretzsch 2014)

Crown maps of monocultures and mixed stands of Norway spruce and European beech and sessile oak and European beech on long-term plots in Germany with eight-radii-crown measurements can be used to illustrate the differences between crown dynamics in intra- and interspecific environments (Table 5.5).

The cpa/sa ratios in Table 5.5 reflect that, except for beech when mixed with oak, all three species can significantly expand their crowns laterally far beyond their stand area when growing in mixed compared with pure stands.

The ratio r_{min}/r_{max} reveals that, compared with the other species, beech crown projection areas are mostly less circular, i.e. more jagged. Mixing significantly increases the rotundity in the case of spruce ($p < 0.001$), decreases the rotundity of beech ($p < 0.001$), and leaves the rotundity of the crowns of sessile oak unaffected.

The crown eccentricity, ecc, is indicated by the standardised distance between the gravity centre of the crown projection area and the tree position (modified after Pretzsch 2014). The ecc values are the highest for beech, especially when growing in mixed stands. Values of ecc = 5.7–7.4 indicate that beeches have plastic crowns for resource capture even distant from their stem position. The measures show that crown morphology can significantly shift from intra- to interspecific competition and trigger the space occupation of the combined species in a species-specific way.

Table 5.5 Lateral crown expansion of individual trees in even-aged mixed versus pure forest stands of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) (above) and sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.) (below)

Species combination		**N. sp. (E. be.)**	**N. spruce**	**N. spruce**	**E. be. (N. sp.)**	**E. beech**	**E. beech**
		Mixed	**Pure**	**Mix/pure**	**Mixed**	**Pure**	**Mix/pure**
n	(trees)	4634	3623		4845	3173	
cpa/sa	($m^2\ m^{-2}$)	1.22 (± 0.095)**a**	0.98 (± 0.042)**a**	1.24	1.84 (± 0.109)**c**	1.32 (± 0.073)**c**	1.39
r_{min}/r_{max}	$m\ m^{-1}$	0.51 (± 0.026)**c**	0.43 (± 0.003)**c**	1.19	0.36 (± 0.027)**c**	0.38 (± 0.003)**c**	0.95
ecc	($cm\ cm^{-1}$)	1.80 (± 0.020)**c**	1.90 (± 0.030)**c**	0.95	5.70 (± 0.060)**c**	4.40 (± 0.060)**c**	1.30
Species combination		**E. be. (s. oak)**	**E. beech**	**E. beech**	**s. oak (E. be.)**	**s. oak**	**s. oak**
		Mixed	**Pure**	**Mix/pure**	**Mixed**	**Pure**	**Mix/pure**
n	(trees)	2326	3173		1959	2888	
cpa/sa	($m^2\ m^{-2}$)	1.48 (± 0.192)	1.32 (± 0.073)	1.12	1.39 (± 0.207)**a**	0.90 (± 0.074)**a**	1.54
r_{min}/r_{max}	$m\ m^{-1}$	0.35 (± 0.004)**c**	0.38 (± 0.003)**c**	0.92	0.38 (± 0.004)	0.38 (± 0.003)	1.00
ecc	($cm\ cm^{-1}$)	7.4 (± 0.110)**c**	4.40 (± 0.060)**c**	1.68	3.30 (± 0.050)**c**	3.10 (± 0.040)**c**	1.06

The data comes from crown projection measurements on fully stocked experimental plots in Bavaria/South Germany

Lowercase bold letters (**a** and **c**) behind the standard errors indicate that Welch two sample t-tests revealed significant differences (at level $p < 0.05$ and $p < 0.001$, respectively) between the species behaviour in mixed versus pure stands

cpa/sa cpa/sa ratio represents crown extension in relation to stand area; r_{min}/r_{max} crown rotundity in terms of the ratio between the largest to shortest radius; *ecc* crown eccentricity indicated by the standardised distance between the gravity centre of the crown projection area and the tree position (Modified after Pretzsch 2014)

5.4.2 Root Morphology and Root-Shoot Allometry

According to the optimal partitioning theory (McCarthy and Enquist 2007), the shape of the tree crown, root system, and the relationship between these depends highly on the resource supply of the plant. Part of the large variation in the root-shoot relationship of plants can be explained by this theory. It predicts that the limitation of a resource leads to the promotion of growth of the plant organ responsible for supplying that critical resource (Comeau and Kimmins 1989; Keyes and Grier 1981).

Changes in the partitioning between root and shoot growth can indicate a modification of environmental conditions through mixing as shown for the rather easily accessible crown growth. Analysis of root-shoot allometry based on tree ring analyses at increment cores from stem and coarse roots can reveal how the root-shoot relationships depend on site conditions (Pretzsch et al. 2012a, b, 2013a, b) and silvicultural treatment (Bauhus et al. 2017d; Pretzsch et al. 2014).

Based on tree ring analysis, the diameter development of coarse roots may be plotted over the stem diameter development for each tree in a double-logarithmic scale. The grey trajectories in the background of Fig. 5.13 show such root-shoot

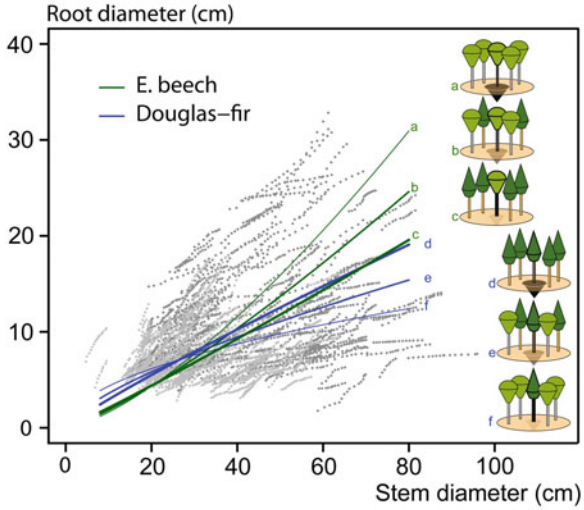

Fig. 5.13 Compared with monospecific stands (lines a and d), in mixed-species stands, the growth of coarse roots in European beech (*Fagus sylvatica* L.) (lines b and c) and Douglas fir (*Pseudotsuga menziesii* Mirb.) (lines e and f) in relation to stem growth is reduced. In monocultures of European beech (line a) and Douglas fir (line d), the allometric relationship between coarse root growth and stem diameter growth is steepest (After Thurm et al. 2016)

The graphs show the results of increment boring at coarse roots and stem of European beech ($n = 85$) and Douglas fir ($n = 90$) in 50–100-year-old monospecific and mixed-species stands on moist and nutrient-rich sites in Southern Germany. For the double-logarithmic allometric model, coarse root diameter = f (stem diameter, mixing proportion, tree species) allometries exemplarily for European beech and Douglas fir grown in monospecific and mixed-species stands (Thurm et al. 2016).

The regression analysis of the individual coarse root diameter-stem diameter trajectories revealed that both European beech and Douglas fir have reduced coarse root growth in mixed compared with monospecific stands (Fig. 5.13, line c versus a and lines f versus d). In both monocultures (Fig. 5.13, lines a and d), the allometric relationship between coarse root growth and stem diameter growth is the steepest, i.e. the investment in roots compared with stem is maximal.

Certainly, the selected coarse roots represent just a small portion of the trees' whole root system, and their development is more sluggish and persistent than that of the ephemeral fine roots. But analogously to the stem which indicates the development of the crown and leaf area, the coarse root diameter reflects the activity of the whole root, since the coarse roots ultimately provide the basic structure and pipe system for the fine roots. So, the coarse root growth might be used as an integrative and non-specific indicator for the root system as a whole.

5.4.3 Effect of Tree Species Mixing on Wood Quality

As both the species-specific morphological plasticity and the tree's spatial constellation within the stand have a specific effect on the tree's morphology and timber quality, we distinguish the basic combinations of both factors shown in Fig. 5.14.

The trees behaviour in different kinds of stands is primarily determined by its species-specific morphological plasticity. We distinguish between low morphological plasticity (e.g. Norway spruce, Douglas fir, sycamore maple, red alder) with apical dominance and rather orthotropic crown extension and label them by an a behind the type (types 1a–3a, upper line in Fig. 5.14). Types 1b–3b indicate species with high plasticity (e.g. European beech, sessile and common oak (*Quercus petraea* (MATT.) LIEBL./*Quercus robur* L.), Scots pine, silver fir) with lower apical dominance and stronger plagiotropic crown extension (types 1b–3b, lower line in Fig. 5.14).

The spatial constellation a tree is exposed to within the stand has also a strong effect on its structural development. We distinguished the three basis types 1–3, characterised by strong lateral restriction (in fully stocked, monolayered pure stand and admixture of species with low crown transparency), vertical restriction (multi-layered pure and mixed-species stands), and low restriction (widely spaced and heavily thinned monocultures, admixture of species with high crown transparency) (Fig. 5.14, from left to right). The constellations on the left (types 1a and 1b) represent rather conservative silvicultural concepts, those in the middle uneven-aged close-to-nature concepts and the results of forest transformation from plantations to more natural and structure stands (types 2a and 2b). The constellations on the right (types 3a and 3b) represent the intensively spaced and thinned contemporary silvicultural concepts for pure and mixed stands.

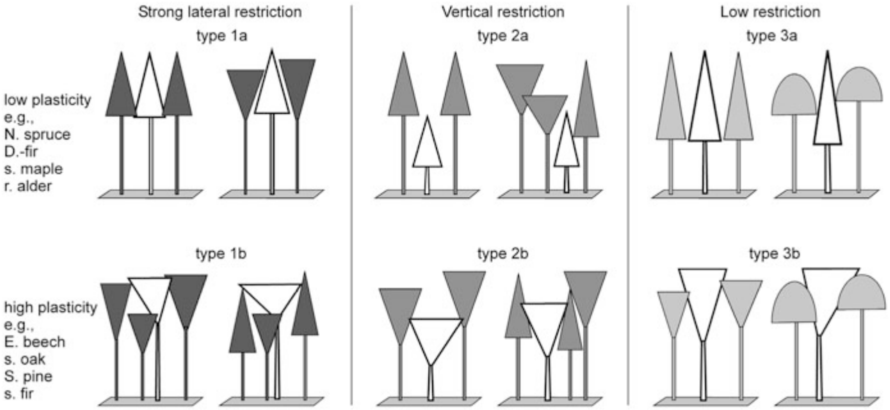

Fig. 5.14 Spatial constellation of a tree with the stand (type 1, strong lateral restriction; type 2, vertical restriction; type 3, low restriction) and the species-specific morphological plasticity (a, low, and b, high) as main drivers of the morphology and timber quality. The resulting six combinations of spatial constellation (from left to right) and morphological plasticity (upper and lower lines, respectively) result in the types 1a–3b which have specific effects on the tree structure and wood quality (after Pretzsch and Rais 2016).
The reacting individual tree in question (white) and its neighbours (grey) in schematic representation. Neighbours drawn in light grey indicate transparent crowns and low competition; neighbours in dark grey indicate low transparency and higher competition

The typology allows to assign also species not considered in Fig. 5.14 to one of these six combinations of plasticity and restriction and predict their reaction in terms of tree structure and wood quality. The behaviour of European larch, e.g. (high plasticity) when monolayered and growing densely associated with European beech, might be assigned to type 1b. The behaviour of Norway spruce (low plasticity) in the understorey of a selection forest of Norway spruce, silver fir, and European beech, e.g., might follow type 2a.

Knowledge of how heterogeneous pure and mixed-species stands come off in terms of quantity and quality of the produced wood is still very limited, as forest research has been rather focused on pure stands in the past. Pretzsch and Rais (2016) reviewed the still rather limited comparative studies on timber quality in mixed versus pure stands. They further reviewed about 100 not direct comparisons but related studies on the morphology of forest stands. As the close connection between morphology and timber quality is well known from many studies in pure stands, morphological and structural properties of trees in mixed stands can be used as proxies for their timber quality.

All in all the number of studies which report a decrease or an increase of timber strength and stiffness in complex stands compared with homogeneous stands were balanced. Knottiness was mostly stronger in complex stands. Wood density behaves indifferently. Distortion, indicated by eccentricity of crown, bending of stems, or irregularity of the tree ring width, is in the majority higher in complex forests.

This rather ambiguous pattern becomes clearer by typifying the findings depending on the species-specific morphological plasticity of the trees and the spatial constellations they are exposed to. When growing in strong lateral restriction in even-aged pure or mixed-species stands (type 1), trees follow a "keep abreast" strategy which results in high-quality timber especially in case of species with low plasticity. Trees in uneven-aged forests with vertically restricted growing space (type 2) often use a "sit-and-wait" strategy which may result in tapering stem shapes, wide and long crowns with low branch diameters, and high wood density. Distortion may be low in case of species with low morphological plasticity but increase with increasing shade tolerance and plasticity. Growth in widely spaced and heavily thinned pure and mixed stands (type 3) may let trees follow the "stabilisation" strategy. Because of their strong dominance, those trees develop tapering stem shapes, knots of big sizes, and wide appearance along the stem axis, as well as lower wood density, especially in case of conifers. Constellations of types 1–3 may also emerge the "transition" strategy, which leads from the "sit-and-wait" stadium to the "keep abreast" strategy. It starts when trees strongly increase their height growth at the expense of the stem diameter growth. It results in slender stems, low knottiness, high wood density, and low distortion, as the tree's main objective is to get access to the upper canopy; this can be achieved just at the expense of lateral expansion of stem and crown.

It is actually not primarily the species mixing which modifies the morphology, structure, and wood quality of the trees but the species-specific morphological plasticity and the structural heterogeneity of the stand. Latter is often higher in mixed than in pure stands and in uneven-aged than in even-aged stands. The more variable the stand structure, the wider the range of wood attributes.

Recently Zeller et al. (2017) used five of the triplets of mature and fully stocked monocultures and mixed stands of Scots pine and European beech (Heym et al. 2017; Ruiz-Peinado et al. 2018) for analysing whether tree species mixing modifies tree ring wood density. Tree ring width of Scots pine was, on average, 14% wider in mixed compared with pure stands. As shown in Fig. 5.15, Scots pine had wider tree rings (+14%) in mixed stands than in pure stands. Tree ring width of European beech did not differ between pure and mixed stands. Tree ring wood density was lower in mixed stands compared to pure stands for both Scots pine (−12%) and European beech (−8%). Future works should further explore those effects of mixing on wood density and consider the consequences for mechanical tree stability, volume-based estimation of overyielding, carbon storage, and wood quality.

5.5 Causes and Mechanisms of Mixing Effects

Productivity losses or gains in mixed compared with pure stands finally result from changes of availability, capture, or use efficiency of resources by the given species assemblage. Benefits in resource supply which are of main interests may be caused by species complementarity and competition reduction or by facilitative interactions.

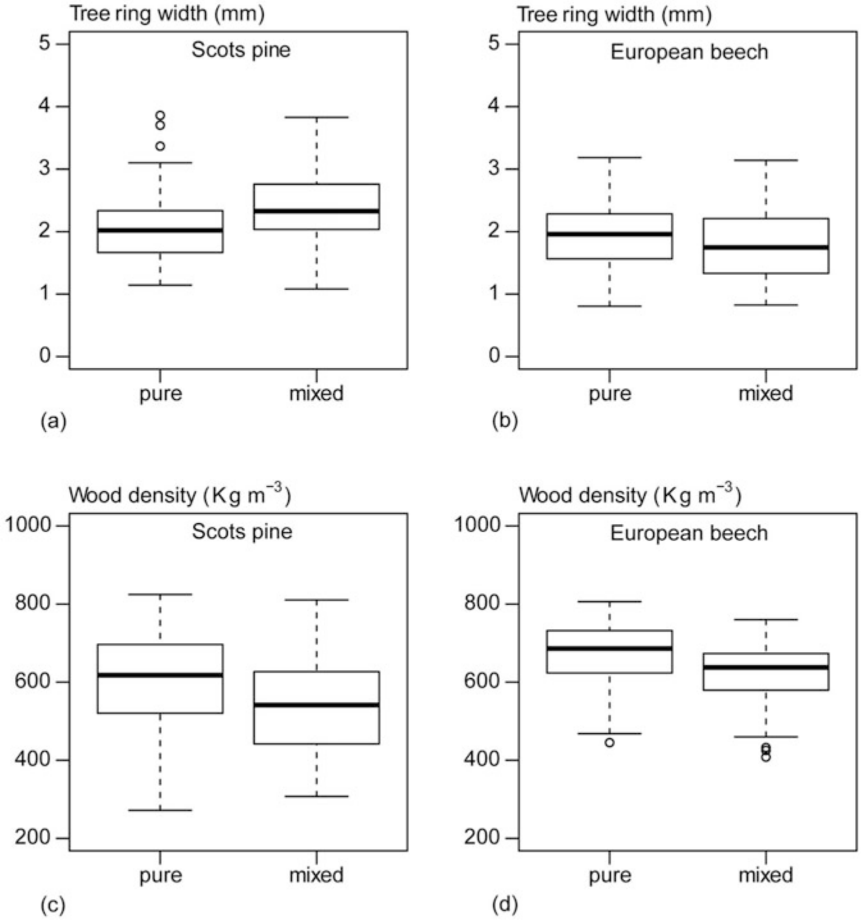

Fig. 5.15 Differences between pure and mixed stands in (**a** and **b**) mean tree ring width of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) and (**c** and **d**) differences in mean tree ring wood density of Scots pine European beech. (Modified after Zeller et al. 2017)

The kind of interaction depends on the species traits and may be modified and modulated by site conditions, stand structure, and silvicultural interferences, which again modify the stand structure. The species' complementarity is obvious when, e.g., light-demanding species are mixed with shade-tolerant, shallow-rooting species with deep-rooting species, fast-growing with slow-growing species or conifers with evergreen species. Facilitation can be caused by atmospheric nitrogen-fixing tree species or by deep-rooting species which cause soil water lift and partitioning in favour of shallow-rooting neighbours.

Whether a given mixture can exploit the potential complementary and overyielding given on a site depends on the stand structure. Obviously, a combination of shade-tolerant and light-demanding species can only exploit the complementarity when the light-demanding species is higher than the shade tolerant and when this pattern is maintained with progressing stand development. Silvicultural interferences may eliminate the mixing effect in those mixtures, where the overyielding is mainly based on a higher light interception and denser canopy structure. The effect of the site conditions on the complementarity and potential overyielding are obvious: overyielding can just be expected if the species combination contributes to reduce the resource limitation; that may be nutrient or water limitation on poor sites or light limitation on fertile sites. The main causes of mixing effects and conceptual models for their interactions are known and presented in the following.

5.5.1 Basic Feedback Loop between Growth, Structure, and Local Environment in Mixed-Species Forest Stands

The conceptual model in Fig. 5.16 clarifies essential plant-plant interactions in monospecific and mixed-species communities. Trees interact with their environment in two ways, via structure and functioning (Hari 1985). The feedback between functioning and environment (FE loop) can be very rapid and temporary, e.g. defence substances are exuded quickly after or nearly simultaneously to the injury or pathogen attack and are reduced after stress release (within-stand environment versus external environmental drivers). Reduction of atmospheric CO_2 concentration or soil water supply by roots and crowns of fast-reacting neighbours can immediately reduce photosynthesis or growth of slower-reacting trees.

The feedback between functioning, structure, and environment (FSE loop), in contrast, is slow and accumulative. The functioning changes the structure (e.g. tree

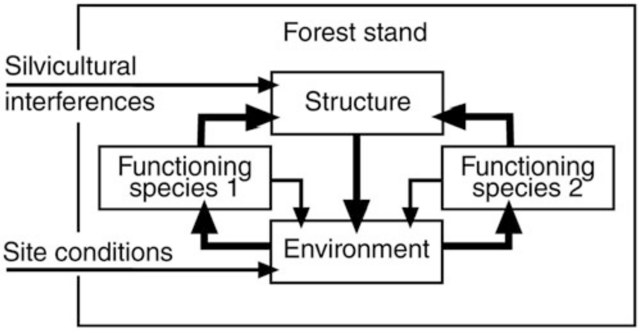

Fig. 5.16 Feedback loop between stand structure (S), environmental conditions (E), and tree functioning (F) in a two-species stand. The outer feedback loops (SEFS loop) structure→environment→functioning→structure (bold arrows) are slow; the inner loops (EFE loop) environment→functioning→environment work faster (After Pretzsch 2014)

size and size distribution) and, via tree and stand structures, the trees' environment. The crown structure, for instance, determines where the water and mineral nutrients from the crown periphery drip to and to what extent neighbours are shaded. The pattern of water drip and shading determines where the roots and crowns of neighbours grow and where they forage. This in turn determines their morphological structure. Trees develop and maintain their root, stem, and crown structure for decades and affect and adapt to their surroundings rather permanently.

The feedback between environment, growth, and structure may be relatively clear in monospecific stands where the species apply similar tricks and traits when appropriating contested resources, adapting to the environment, and modifying the stand structure. In mixed stands with two species as shown in Fig. 5.16 or with even more species, interactions and their effects on growth, structure, and environment may be more varied. Mixed species modify their environment to their own benefit, e.g. by overtopping the neighbouring crowns or penetrating neighbouring roots in order to improve access to contested resources and acclimation to the environment altered by their neighbours. The principle feedback remains the same when neighbours belong to different species; however, their tricks and traits to modify their environment may be different, so that a broader range of reaction patterns, structures, and changes to the environment may occur.

The subsequent analyses of tree structure and tree growth in mixed versus monospecific stands addresses the two key elements of the feedback loop. Long-term experiments provide retrospective information on growth and structure but rarely time series on environmental variables such as light profile, nutrient supply, or water uptake of trees in mixed versus monospecific stands. Therefore, the effect of mixing on the local environment is less known and understood than the effect on structure and growth. However, future approaches will close this knowledge gap to enhance understanding of the feedback and underlying mechanism as a whole (Binkley et al. 2004; Pretzsch et al. 2015b).

5.5.2 The Relevance of Environmental Conditions

The complementarity of the species and the potential for overyielding compared with their productivity in pure stands can change with site conditions. In this section we will show how the potential overyielding depends on the environmental conditions. In the next section we show that the stand structure determines to what extend a given species assemblage can exploit the species-specific potential of complementarity under given site conditions.

Many studies found strong mixing reactions in terms of overyielding on poor sites (Pretzsch et al. 2013a) and in low-growth years (del Río et al. 2014). Other studies report opposite reaction patterns or site invariant mixing reactions (Pretzsch et al. 2015a) or even mixing effects increasing with water and nutrient supply (Forrester 2017; Jactel et al. 2018; Thurm and Pretzsch 2016). We hypothesise that the kind of mixing reaction and level of overyielding mainly depend on the potential of the

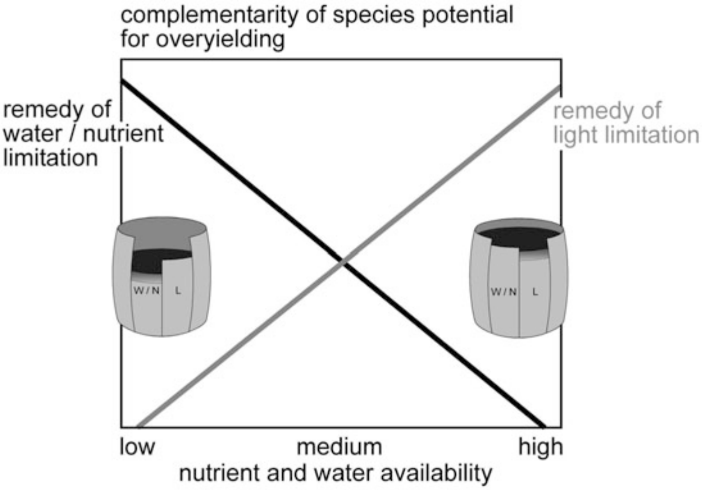

Fig. 5.17 Hypotheses on the dependency of species complementarity and overyielding from site conditions. We hypothesise that the kind of mixing reaction and level of overyielding mainly depends on the potential of the species assemblage to remedy the respective growth limiting factor on a given site. So, the mixing reactions and their change along a gradient of site conditions depend on the respective limiting factor and the species' potential to overcome the limitation. (Modified after Forrester 2017)

Decreasing black line: Complementarity could decrease as soil nutrient availability increases when interactions increase nutrient availability (e.g. accelerated rates of nutrient cycling). This will be a more useful process on sites where those nutrients are limiting

Increasing grey line: Complementarity could increase as competition for light becomes more intense when interactions increase light interception or light-use efficiency. This type of interaction would be less useful if nutrients or water limits growth, but its usefulness should increase as soil resource availability increases (or climatic conditions become more favourable).

species assemblage to remedy the respective growth limiting factor on a given site. So, the mixing reactions and their change along a gradient of site conditions depend on the respective limiting factor and the species' potential to overcome the limitation (Fig. 5.17).

Probably, complementary in mineral nutrients and water exploitation is most effective and growth accelerating on sites with mineral nutrients and water limitation. With increasing mineral nutrients and water supply the effect of this complementary may decrease (Fig. 5.17, decreasing black line). Complementary in light ecology is rather useless when mineral nutrients and water are growth limiting but may increase in effectivity the better the mineral nutrients and water supply, and the more the light is growth limiting (Fig. 5.17, increasing grey line). In Fig. 5.17 left and right, we used the barrels introduced by Liebig (1855) and applied by Mitscherlich (1909) for illustrating how the growth limiting factor changes from mineral nutrients and water (W/N) on poor sites to light (L) on more fertile sites.

5.5.3 The Modifying Role of Stand Structure

The growth and yield of species in monospecific stands, i.e. when growing without interspecific competition, depend mainly on the site conditions and especially on the respective resource limitation. Productivity of most species is low on dry and nutrient poor sites and at maximum on moist and nutrient rich sites. So, the production optima of various species are rather similar under intraspecific competition. The concept of resource limitation and unimodal relationship between resource supply and productivity (Liebig 1855; Mitscherlich 1909) is less useful in mixed-species stands.

When growing in mixed-species stands, the size differences and competitive interactions between the species come into play and determine their growth much more than the prevailing site conditions. Even if the site conditions enable maximum productivity for a species in pure stand, it might be outcompeted in mixture by another species which is faster in size growth, shading, or more expanding in crown expansion. The site conditions for maximum growth in pure stands (production optimum) often differ considerably from the site conditions where a species achieves its maximum occurrence and fitness in the interplay with other species (ecological optimum). This difference between both becomes essential for understanding, modelling, and silvicultural treatment of mixed-species stands.

The difference becomes obvious by the well-known fact that Norway spruce and Scots pine achieve their maximum productivity which is far above other species on moist and fertile sites in low and hilly regions of Central Europe. However, under natural conditions, in mixture, and without promotion, both species would be outcompeted by less productive but more adapted species such as European beech, sessile oak, or common ash (see Fig. 5.19 and Körner 2002).

In contrast to development in pure stands, in mixed-species stands the competitive status of a species, e.g. the height in relation to other species, may become more relevant for its growth than the site conditions (Fig. 5.18).

A useful reference for prediction of mixing effects and designing tree species mixing is the species-specific height curves in pure stands on the respective site. Very different are especially the height curves of light-demanding fast-growing and shade-tolerant slowly growing species with large final heights (Fig. 5.19a). Intersection of the height curves indicates a change of the competitive relationship and especially when shade tolerant overtop light demanding may result in suppression or even dropout of the species with the lower final height (Fig. 5.19b). In this example sessile oak would need much promotion by cutting out neighbouring beeches in order to keep it in the mixture.

A reduction of the interspecific competition indicated by the intersection of the height curves may be achieved by a temporal or spatial decoupling of their growth; temporal decoupling means that the faster-growing species may be established some decades later than the slow-growing one, and spatial decoupling may be achieved by establishment in groups or clusters, so except at the borderlines both species develop mainly under intraspecific competition. Figure 5.19c shows how temporal

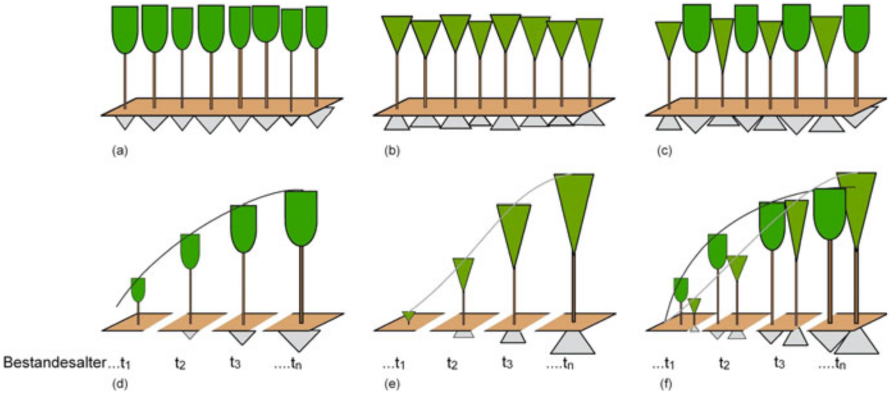

Fig. 5.18 Most relevant for the development of species in a mixed stand is its height in relation to the admixed species. A lead in height development can enhance the own productivity and slow down the development of neighbouring species. If two species such as Scots pine and European beech with complementary traits and structure (**a**, **b**) are mixed, this can result in a stratification in the canopy space (**c**). The height curves known from monocultures (**d**, **e**) can get modified by the species interaction (**f**). (Modified after Pretzsch and Forrester 2017)

decoupling may avoid the intersection of height curves in too early stand development phase. Tree species with similar height growth curves and shade tolerance such as Norway spruce, silver fir, and European beech enable a continuously stable mixture as all contributing tree species can stay in the play. A model example is mixed mountain forests in the submontane and montane altitude of the Alps (see Fig. 5.1d).

5.5.4 *The Main Mechanisms*

Complementary exploitation of crown and root space: Any changes in tree crown morphology and canopy structure in interspecific versus intraspecific environments suggest a modification of the trees' space occupation, resource capture, and productivity. Of special interest is a wider crown extension as this indicates a competition reduction and an increase in light interception and may also contribute to overyielding of mixed compared with monospecific stands. Changes in crown structure and allometry underline that the mixing effect goes beyond a merely additive effect where the species' behaviour in terms of structure and growth remains similar to that in the monoculture (Barbeito et al. 2017).

In temperate forests where tree growth is primarily limited by light, canopy space filling may be denser and light interception higher in mixed than in monospecific stands. Especially when their crown shapes are complementary, the crown expansion may be wider (Fig. 5.20d), the tree packing density may be higher (Fig. 5.20e),

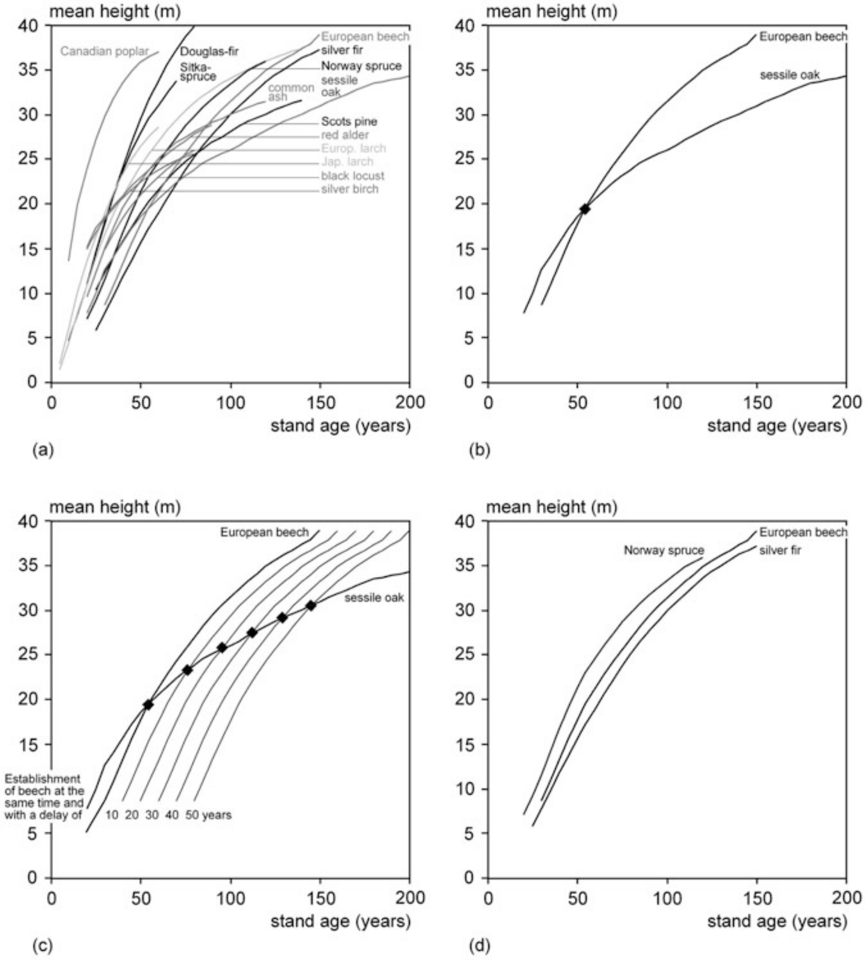

Fig. 5.19 Essential for the development of a species in mixture is the course and final tree height in relation to the neighbours. Based on mean height curves of fully stocked pure stands on very good sites (Schober 1975), the graph illustrates how to recognise and avoid interspecific competition

(**a**) Light-demanding species with a fast height development and low final heights (silver birch, poplar, alder) may be outcompeted when even-aged mixed with shade-tolerant slow developing species with larger final heights (Norway spruce, European beech, silver fir)

(**b**) The point of intersection between the height curves of mixed species indicates the development of their competitive relationships and the need of silvicultural interventions and suggests how to reduce competition by uneven-aged establishment. In the case of sessile oak and European beech, oak will need promotion from medium stand age onwards

(**c**) In order to reduce the suppression of the light-demanding species with the lower final height, in this case the suppression of oak by beech, the latter may be established 10–50 years later. Even when established 50 years later, beech can still catch up with oak when both are growing on excellent sites

(**d**) The rather simultaneous course of mean height of Norway spruce, silver fir, and European beech and their shade tolerance may guarantee their coexistence in the mixed mountain forests or both reactions may be combined (Fig. 5.20f) in mixed stands compared with the crown extensions found in monocultures (Fig. 5.20a–c). Similar complementarity with regard to their root morphology may increase the benefit of inter- compared with intraspecific neighbourhoods.

The cpa/sa relationship (for explanation, see Table 5.5) can become greater in mixed stands (Fig. 5.21b) and the degree of crown closure – and therefore the crown closure and the sum of crown projection areas – may be higher than in monocultures (Fig. 5.21a). Larger crowns and denser canopy space filling can increase the tree and stand growth.

Analogously, a complementary root morphology may benefit inter- compared with intraspecific neighbourhoods in the root space.

Hydraulic lift and hydraulic redistribution: Especially in dry years and on dry sites where water is the limiting factor, processes in the root space become decisive for tree growth and survival. However, outcomes under drought conditions may turn into benefits for some of the associates. One such phenomenon is the well-described "hydraulic lift" or "hydraulic redistribution" of water in woody plants, particularly observable in arid conditions, through deeply extending root systems (Fig. 5.22a), which release water at night into surface-near soil horizons of low water potential (Fig. 5.22b) as described in detail by Caldwell and Richards (1989) and Prieto et al. (2012). Once released, such water represents an external storage capacitance for the deep-rooting plant but concomitantly enables survival of neighbouring shallow-rooting plants as the profiteers. The resulting benefit is not an active support provided by the deep-rooting plant but occurs indirectly as an emergent feature of the specific species association under a specific site scenario. In such a case, competition turns into facilitation, which denotes an indirectly mediated, functional emergence between neighbouring plants. One or several of the associates may benefit with regard to water availability and growth.

Increased availability of mineral nutrient supply through deep-rooting or atmospheric N_2 fixation: In mixed stands one tree species may benefit from another species which can exploit mineral nutrients in deeper root layers (Fig. 5.23a) or can fix atmospheric N_2 (Fig. 5.23b). In both cases, mineral nutrients are procured by a benefactor species and partly transferred to the other through litter fall. Thus, the additional nutrients are socialised among the neighbouring trees of the benefactor independently of their species. An additional benefit may come from root channels abandoned by one species and used by the other for penetrating compacted soil

Fig. 5.19 (continued) Height curves of sessile oak (*Quercus petraea* (MATT.) LIEBL.), European beech (*Fagus sylvatica* L.), red alder (*Alnus glutinosa* (L.) GAERTN.), common ash (*Fraxinus excelsior* L.), silver birch (*Betula pendula* ROTH), black locust (*Robinia pseudoacacia* L.), Canadian poplar Marilandica (*Populus marilandica* BOSC.), Norway spruce (*Picea abies* (L.) KARST.), Sitka spruce (*Picea sitchensis* (BONG.) Carr.), Douglas fir (*Pseudotsuga menziesii* MIRB.), silver fir (*Abies alba* MILL.), Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* MILL.), Japanese larch (*Larix leptolepis* GORD.)

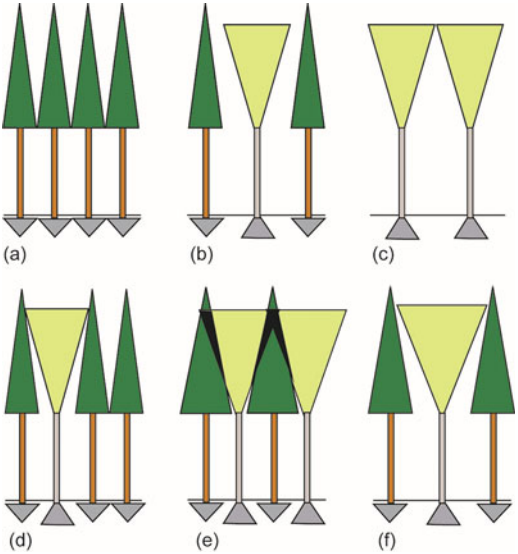

Fig. 5.20 Potential effects of species mixing on the canopy and root space filling when tree crowns have complementary shapes. When two species with complementary crown shapes (**a**, **c**) retain the same shape and space occupation in mixed-species stands – as is common for monospecific stands – the space filling in mixture may be simply additive (**b**). However, in many cases, species mixing enables a wider crown expansion (**d**), higher stand density (**e**), or a combination of both (**f**). The cases (**d**–**f**) indicate a multiplicative mixing effect through denser canopy space filling. (Pretzsch 2014)

layers and reaching resources in deeper and otherwise inaccessible soil layers (Bauhus and Messier 1999; Gaiser 1952; Puhe 2003; Stone and Kalisz 1991).

Temporal complementarity of niches, resource use, and growth: Many studies show clear differences in the course of growth between the species across their lifetimes (Assmann 1970, p. 45) but also within a single year (Pretzsch 2005; Schober 1950). This asynchrony in growth entails a temporal diversification in resource uptake which can release stress and stabilise productivity (del Río et al. 2017; Forrester 2014).

For instance, Norway spruce may profit from a released competition for water in early spring when European beech is still leafless and lives from the reserves of the previous year (Fig. 5.24). In this period, photosynthesis and growth of spruce may profit from higher temperatures and light supply till beech sprouts in April/May. Afterwards, European beech may profit from the mixture in relation to the monospecific stand as the admixed Norway spruces have shallower roots. During the main growing season, scattered European beeches in the mixture with Norway spruce may have greater water availability than in monocultures of beech as the interspecific competition with neighbouring spruces is lower than the intraspecific competition with beech. This may explain why beeches in interspecific environments grow much better than those beside beeches, especially in drought years (Goisser et al. 2016).

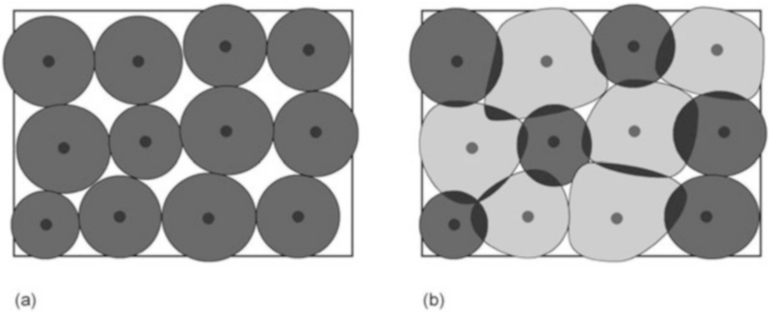

Fig. 5.21 Schematic representation of canopy pattern in monospecific versus mixed stands. (Modified after Pretzsch 2017b)
(**a**) Rather circular crowns in monospecific stand with about 5–10% uncovered space in between, a crown cover of 90–95% and sum of crown areas below 100%
(**b**) More irregular crown shapes in mixed stand with scarce uncovered space in between, crown cover close to 100%, and multiple crown overlap resulting in a sum of crown areas of greater than 100%

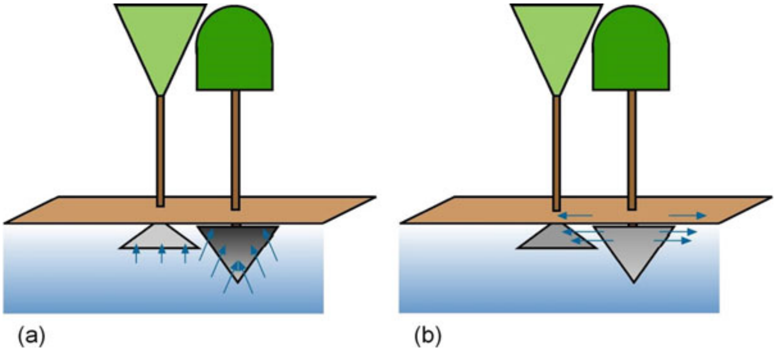

Fig. 5.22 If shallow-rooting species are mixed with deep-rooting species, they can benefit from hydraulic redistribution (Modified after Pretzsch 2017b). (**a**) During the day when stomata are opened, both species take up water for transpiration. (**b**) Dry soil conditions may extract water from the deep-reaching roots, especially during the night when water flow is reduced. Shallower-rooting trees may benefit from this redistribution in terms of water supply and growth. (Caldwell and Richards 1989)

Analogously, temporal diversification of space occupation during stand development may relax resource competition. It occurs, for example, in species assemblages of shade-tolerant and shade-intolerant, shallow- and deep-rooting, and early- and late-successional tree species. For given site conditions, species 1 and 2 in Fig. 5.25 may access resources in different spaces or at different times.

Modification of growth partitioning and allometry of trees in inter- versus *intraspecific neighbourhoods:* In order to acclimatise to an interspecific neighbourhood, trees species may change their growth partitioning in mixed-species

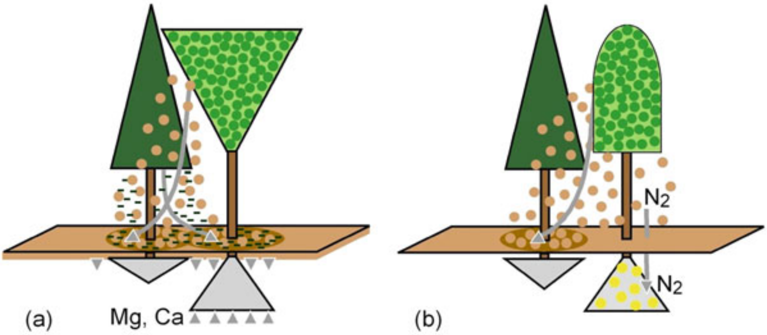

Fig. 5.23 In assemblages of tree species with different behaviours of mineral nutrient exploitation, one species may facilitate the other through socialisation of nutrient supply via leaf and needle turnover. (Modified after Pretzsch 2017b)
(**a**) Shallower-rooting species may benefit from deep-rooting neighbours because they act as a “mineral nutrient pump”. (Rothe 1997; Rothe and Binkley 2001)
(**b**) Species with the potential for atmospheric N_2 fixation may facilitate neighbouring species that lack this ability, especially when growing on N-limited sites. (Forrester et al. 2006, 2007)

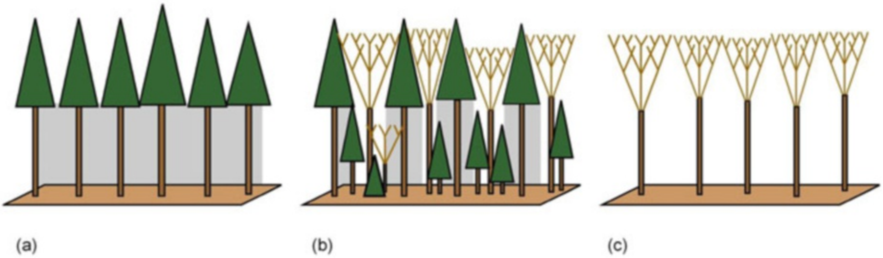

Fig. 5.24 Temporal complementarity of resource use and growth when mixing evergreen species (**a**) with deciduous tree species (**c**) (Modified after Pretzsch 2017b). In mixtures of both species (**b**), conifers can start growing before the sprouting of their deciduous neighbours. This asynchrony may promote smaller conifers in particular and enrich stand structure and stand productivity. (Schober 1950)

stands compared with monospecific stands. Most of the comparisons between the productivity of mixed and pure stands are based on stem volume production (Liang et al. 2016; Pretzsch et al. 2015a). Comparison based on total biomass production may produce different results, as tree species mixing can change stem-crown allometry (Bayer et al. 2013), root-shoot relationship (Thurm et al. 2016), and also tree ring width and wood density (Zeller et al. 2017) as illustrated in Fig. 5.26.

An increase in crown in relation to stem size in mixed-species stands as reported by Dieler and Pretzsch (2013) and Pretzsch (2014) would mean that the overyielding would be even higher when calculated for the total above-ground volume of mixed versus pure stands. However, the decrease of root in relation to shoot growth as reported by Thurm et al. (2016) and in Sect. 5.4.2 as well as the decrease of wood

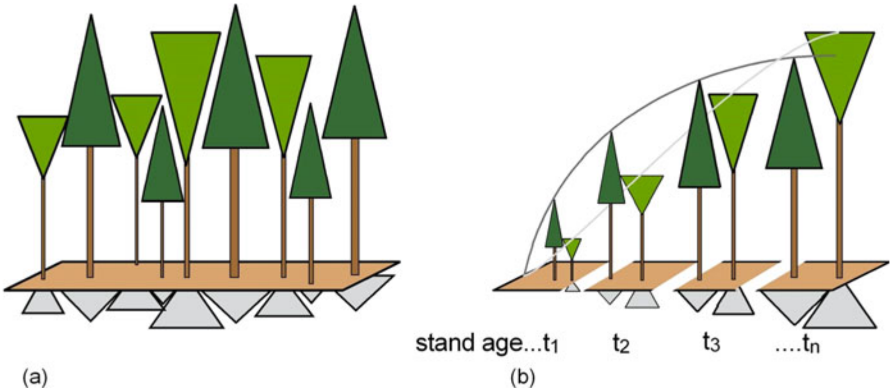

Fig. 5.25 Complementary occupation and packing density in the canopy and root space found in one stand development phase (**a**) may change over time (**b**). In the mixture shown on the right (**b**), conifer is initially ahead but later lags behind in height growth. However, due to the species-specific crown development, complementary space occupation may result in all stand development phases. (Modified after Pretzsch 2017b)

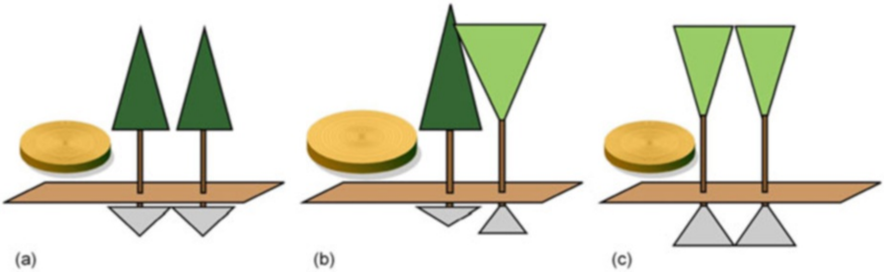

Fig. 5.26 Tree species mixing may modify the growth allocation and allometry in mixed (**b**) compared with monospecific stands (**a**, **c**). Mixing may modify the crown size, the root-shoot relationship, the tree ring width, and the wood density. So, comparison between mixed and monospecific stands based on the stem volume growth may be misleading. (Modified after Pretzsch 2017b)

density revealed by Zeller et al. (2017) would lower the overyielding of mixed versus pure stands when calculated for the total biomass growth. Ongoing works on within-tree growth partitioning in mixed versus pure stands will clarify how mixed stand productivity compares with that in pure stands when calculated for the stem volume productivity, which is of primary interest for forestry. They will also clarify how mixed stand productivity compares with pure stands based on their total biomass production, which is relevant for ecosystem understanding and carbon balance.

The presented tree properties emerging when growing in interspecific in contrast to intraspecific neighbourhoods go beyond an acceleration or reduction of growth velocity, i.e. a quicker tree and stand development. Rather, they can change the trees' structure and space requirement. The presented tree properties emerging in interspecific in contrast to intraspecific competition indicate complementarity in use of above- and below-ground resources.

Beyond the increased productivity, the wider extension of tree crowns and multiple crown overlap in mixture can increase the growth resilience after disturbances, as gaps are smaller or can be closed more quickly (Bayer and Pretzsch 2017). Properties emerging in mixed but not in monospecific stands such as increase in crown size, change in the crowns' space filling pattern, reduction in growing area requirement, and increase in tree productivity are crucial for appropriate estimation of maximum density, silvicultural treatment, and dynamic modelling of mixed-species stands. Because of their size, firm position, and longevity, trees are the founder species in ecosystems and determine the living conditions of many ecosystem characteristics, functions, and services. So, the effects of mixing on tree and furthermore on stand structure have far-reaching effects on most ecosystem properties.

5.6 Perspectives

Essential for designing mixed-species stands are growth models and simulators which integrate the mixing effects and mechanisms revealed in the previous sections. The concepts for such models are on the way (Forrester 2017; Pretzsch et al. 2015b). In this section we stress which knowledge is still missing and how to acquire it by further research. Due to the complexity of the task and the variety of options, the design of mixed-species forest stands and the development of goal-oriented quantitative silvicultural prescriptions depend on appropriate models and simulators and algorithms for silvicultural regulations. At the end of this section, we finally stress how to translate the model-internal algorithms in guidelines and prescriptions with a level of complexity sufficient for regulating mixed-species stands but not overstraining forest practitioners.

5.6.1 Modelling and Simulation as Prerequisite for Developing Silvicultural Guidelines

For monocultures the silvicultural guidelines for appropriate and goal-oriented stand establishment, tending and thinning can be based on scenario analysis with proven growth models (Pretzsch et al. 2015b). Those growth models and simulators are finally based on and parameterised with data from long-term experimental plots or inventory data. As equivalent models for mixed-species stands are missing or at best in development so far, guidelines for the design of mixed-species stands are often based on models for monoculture, e.g. on yield tables, assuming that mixed stands behave like monocultures and their growth and structure equals the weighted mean of neighbouring monocultures. Or the guidelines are simply normative, e.g. they focus on the tending, fostering, and harvesting of 100 crop trees per hectare, without taking into consideration whether those 100 trees over- or underexploit the site-specific capacity (Schröpfer et al. 2009, Utschig et al. 2011). In this regard most thinning prescriptions for mixed-species stands are rather vague, qualitatively formulated, and hardly goal-oriented.

The comparison between the growth and structure of mixed-species stands with the weighted mean of monocultures shown in the previous sections for the stand, size distribution, and the tree level revealed significant mixing effects. The causes of the mixing effects and the underlying mechanisms are far from being understood. We are still far from accepted general rules or laws as they are available for monospecific stands. However, the significant multiplicative mixing effects show that the dynamics of mixed-species stands cannot be simply predicted by models for monocultures. We found that mixed stands can produce by 10–20% more, become by 20–30% denser, or trigger stem growth with lower wood quality. Thus, for design of mixed-species stands, we need models which take into consideration such relevant mixing effects.

Pretzsch et al. (2015b) reviewed the following four main principles for deriving and predicting mixed-species forest growth by models.

First, deriving the growth of mixed-species stands as a weighted mean of monocultures using models of the respective species
Second, an indirect incorporation of mixing effects in individual-tree growth models by integration of species-specific competition indices
Third, a direct incorporation of mixing effects using multipliers affecting growth rates and stand density
Fourth, a process-based representation of mixing effects by incorporating within-stand environmental conditions, species-specific structures, and resource uptake and availability

For all four approaches, there are still knowledge gaps which need to be remedied by further research.

5.6.2 Future Research Directions for Better Understanding, Prediction, and Scenario Calculations

As forest science was focussed on monocultures in the past, there is still a lack of mixed stand experiments for both analysing and training (Bauhus et al. 2017b; Pretzsch and Zenner 2017; Ruiz-Peinado et al. 2018). We see a couple of further research priorities which can serve for improving knowledge and models and pave the way from analysing to designing mixed-species forest stands. In the following we stress to our view the most important knowledge gaps for modelling and regulating mixed-species stands.

1. Most studies so far focus on the most relevant two-species combinations (e.g. spruce-beech, oak-beech); however, combinations such as pine-oak, larch-beech, fir-beech, or spruce-fir-beech and pine-beech-oak are hardly analysed so far. Here we need new experiments for quantifying the mixing effects on tree and stand growth. Whereas most growth and yield studies focus on two-species mixtures and even-aged stands, experiments, inventory data analyses, and modelling should be extended to mixture with $n > 2$ species, uneven-aged stand structures, and nitrogen-fixing and exotic tree species.
2. We have just preliminary concepts for predicting the effect of site conditions on the species interaction, i.e. on the competition and facilitation between given species assemblages. New long-term experiments, inventory data should contribute to better understand the change of mixing effects along ecological gradients.
3. As forests stands can be exposed to climate trends and events, we need a better understanding of how, e.g., drought or storm affects mixed compared with monospecific stands. Future experiments, inventory data analyses, and modelling should further fathom the potential of mixed stands and specific species assemblages for risk resilient forestry under climate change.
4. It is an open question to what extend species identity and stand structural traits are behind mixing effects such as overyielding, crown extension, or overdensity. Disentangling the effects of compositional and structural diversity in mixed, uneven-aged forests is relevant for both theory development and silvicultural management of mixed-species stands.
5. Mixing effects can change with species proportion (20:80, 50:50, etc.), mixing patterns (individual tree mixture, group mixture, etc.), and age structure (even-aged, tow-cohort type, etc.). New experimental plots should better quantify (Dirnberger et al. 2017) and cover those mixing aspects as experimental factors (Pretzsch and Zenner 2017).
6. Although mixing can considerably change tree shape, allometry, stem form factor, etc., most studies and models so far apply tables, factors, and equations developed for monocultures to mixed-species stands. In order to get forward here, we need individual tree structure and biomass analyses which take into consideration the local environment, disentangle the mechanisms controlling the effect of mixing on tree allometry, and enable to predict the tree and wood attributes in dependence on tree size and the structural growth constellation of the tree within the stand (Forrester et al. 2017).
7. Beyond growth and yield characteristics, many other forest functions and services such as water consumption, carbon sequestration, protection against erosion, and the trade-offs between the various functions need to be better analyses and implemented in models. This will enable design of silvicultural prescriptions regarding growth and yield and in addition many other functions by means of scenario analyses.

8. Most studies so far focused on the mixing effect on stand productivity in terms of mean annual growth or total yield. However, further yield components such as height, diameter, basal area, and mortality need further investigations.
9. The effect of mixing on tree structure and wood density needs further research; it is essential to assess the wood quality of mixed stands dominating in the future (Pretzsch and Rais 2016). Future silvicultural guidelines should integrate wood quality aspects into in order to increase not just quantity but also the quality of wood in mixed compared with pure stands.
10. Most comparisons between mixed- and monospecific stands focused on productivity; however, for forest management, many other forest functions and services are highly relevant for decision-making (Bauhus et al. 2017c). So, future research should consider, e.g., water provision, wood quality, carbon storage, non-wood products, social aspects, and also the trade-off between productivity and ecological services.

5.6.3 From Model Algorithms to Practical Guidelines

Apart from some rather normative future crop tree concepts, there are hardly any quantitatively based guidelines available for establishment, thinning, and regeneration of mixed-species stands. The findings in the previous sections regarding, e.g., niche complementarity, allometry, size and growth partitioning, mortality, overyielding, and overpacking should be used to develop and establish quantitative guidelines for mixed-species management via model application and scenario calculations. Silvicultural prescriptions derived by simulation and scenario analyses finally need to be translated into guidelines which are sufficiently but not too complex for forest practice. Here we see a further need for research work. Those algorithms for regulation of mixed stands which are implemented into models cannot be provided 1:1, i.e., in the same level of complexity to forest managers. They rather need to be simplified.

The main elements of simplified guidelines and prescriptions for mixed-species stand management may be rules for (i) choosing species with appropriate complementarity; (ii) designing the temporal or spatial association/separation of the associated species when establishing mixed-species stands; (iii) regulating mixing proportion, mixing pattern, and vertical structure; (iv) regulating stand density; and (v) scheduling individual tree release by thinning. The guidelines for practice need to be equivalent to the algorithms integrated in the models for guideline development by simulation; however, they have to be more practical and less complex. For further silvicultural conclusions, see Mason et al. (2018), Pach et al. (2018), and Pretzsch and Zenner (2017).

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Chapter 6
Silviculture of Mixed Forests: A European Overview of Current Practices and Challenges

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Abstract Currently, about 70% of the forest land in Europe is covered by stands composed of two or more tree species. The similar situation can be found outside Europe too. While forest management of monocultures is well described,

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multispecies forests still need a better understanding to develop appropriate forest practice. Managing mixed forests can be more complex than managing monocultures because of the need to optimize the provision of multiple benefits according to the societal demands including sustaining biodiversity and ecosystem functioning.

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In this chapter we are going to present (1) the most important and well-described tree species combinations found in each participating countries taking biogeographical region in Europe into account, (2) the main management objectives of those mixtures, (3) the silvicultural approaches that are available for the particular

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mixed-species forests and (4) the main challenges experienced in mixed-species forest management. We synthesized information about management of mixed-species forests based on questionnaires received from both European countries and few countries from outside Europe participating in COST Action 'EuMIXFOR'. The survey revealed that (i) the main management objective in the analysed mixtures is valuable timber production followed by protection of soil and water and protection of forests against disturbances, (ii) the uniform shelterwood is the most widespread regeneration method followed by the clear-cutting and the irregular shelterwood system, (iii) the crown thinning followed by low thinning is the most frequent thinning method, and (iv) the main challenge of management is high game pressure and the lack of management rules covering mixture growth and taking into account both species functional traits and site conditions.

Abbreviations

Latin Names of Tree Species

Aa	*Abies alba* Mill.
Aad	*Arbutus andrachne* L.
Ac	*Abies cilicica* Ant. and Kotschy Carriére
Ach	*Austrocedrus chilensis* (D.Don) Pic.Serm. and Bizzarri
Ad	*Arceuthos drupacea* Labill.
Ag	*Alnus glutinosa* Gaertn.
An	*Abies nordmanniana* (Steven) Spach
Ap	*Acer platanoides* L.
Aps	*Acer pseudoplatanus* L.
*A*spp	*Acer* spp.
Au	*Arbutus unedo* L.
Bpe	*Betula pendula* Roth
Bpu	*Betula pubescens* Ehrh.
*B*spp	*Betula* spp.
Ca	*Cedrus atlantica* (Endl.) Manetti ex Carrière
*Ca*spp	*Carpinus* spp.
Cb	*Carpinus betulus* L.
Cl	*Cedrus libani* A. Rich.
Co	*Carpinus orientalis* Mill.
*Cr*spp	*Crataegus* spp.
Cs	*Castanea sativa* Mill.
Cse	*Cupressus sempervirens* L.
*E*spp	*Eucalyptus* spp.
Fa	*Fraxinus angustifolia* Vahl
Fe	*Fraxinus excelsior* L.
Fon	*Fraxinus ornus* L.
Fot	*Fagus orientalis* Lipsky

Fs	*Fagus sylvatica* L.
*J*spp	*Juniperus* spp.
Ld	*Larix decidua* Mill.
*L*spp	*Larix* spp.
Nan	*Nothofagus alpina* (Poepp. and Endl.) Oerst.
Nd	*Nothofagus dombeyi* (Mirb.) Oerst.
No	*Nothofagus obliqua* (Mirb.) Oerst.
Oc	*Ostrya carpinifolia* Scop.
Pa	*Picea abies* [L.] Karst
Pb	*Pinus brutia* Ten.
Pce	*Pinus cembra* L.
Pco	*Pinus contorta* Dougl. ex Loud.
Ph	*Pinus halepensis* Mill.
Pm	*Pseudotsuga menziesii* (Mirb.) Franco
*Pm*spp	*Pinus mugo* spp. Turra
Pn	*Pinus nigra* Arn.
Po	*Picea orientalis* (L.) Peterm.
Pp	*Pinus pinea* L.
Ppr	*Pinus pinaster* Aiton
*Pr*spp	*Prunus* spp.
Psi	*Picea sitchensis* (Bong.) Carrière
*P*spp	*Pinus* spp.
Psy	*Pinus sylvestris* L.
Qce	*Quercus cerris* L.
Qco	*Quercus coccifera* L.
Qfa	*Quercus faginea* subsp. *baetica* (Webb) Maire
Qfr	*Quercus frainetto* Ten.
Qi	*Quercus ilex* L.
Qp	*Quercus petraea* (Matt.) Liebl.
Qpu	*Quercus pubescens* Willd.
Qpy	*Quercus pyrenaica* Willd.
Qr	*Quercus robur* L.
Qrt	*Quercus rotundifolia* Lam.
Qs	*Quercus suber* L.
*Q*spp	*Quercus* spp.
Tc	*Tilia cordata* Mill.
*T*spp	*Tetraclinis* spp.
*T*spp	*Tilia* spp.
Um	*Ulmus minor* Mill.

Silvicultural Systems

CC	Clear-cutting system
CO	Coppice system
CS	Coppice-with-standard system
GS	Group selection system

IH	Individual tree harvesting
IS	Irregular shelterwood system
PCF	Patch clear felling
SE	Selection system
SH	Shelterwood system
SS	Single tree selection system

Types of Regeneration

AP	Artificial regeneration by planting
AS	Artificial regeneration by direct seeding
NR	Natural regeneration from seeds
VR	Vegetative regeneration

Release Treatments

B	Brushing
C	Cleaning
L	Liberation
W	Weeding

Thinning Methods

CRT	Final crop thinning
CT	Crown thinning (thinning from above)
FT	Free style of thinning
IT	Intermediate thinning (mixture of crown and low thinning)
LT	Low thinning (thinning from below)
SVT	Selective thinning (the most competitive trees in relation to crop tree are cut regardless their position in the stand)

Other Intermediate Treatments

FE	Fertilization
PF	Prescribed fire
PR	Artificial pruning
SLC	Salvage cutting
SNC	Sanitation cutting

All Tables

L	Limited
N	No treatment
NA	Not applicable
ND	Not documented (lack of information)
Y	Yes

6.1 Introduction

Timber production was the main objective of forest management in Europe during the last century (Bengtsson et al. 2000; Farrell et al. 2000; Gamborg and Larsen 2003; Puettmann et al. 2009). More recently, the increasing recognition of the important role of forests in providing non-timber goods and services such as soil protection, water quality improvement, wildlife habitat, biodiversity, climate change mitigation, recreational opportunities as well as many others has revitalized interest in forest management practices which favour structural diversification of the stands and the development of mixed forests (Battles et al. 2001; Decocq et al. 2004; MEA 2005a; Rametsteiner et al. 2009; Bravo-Oviedo et al. 2014; Shua et al. 2015). Research has also increased our understanding of how biodiversity influences the functioning of ecosystems and affects the provision of ecosystem goods and services (MEA 2005a, b; Hooper et al. 2005; Balvanera et al. 2006; Leuschner et al. 2009; Gamfeldt et al. 2013). Evidence suggests that certain species combinations show complementary resource use, with positive consequences for productivity (Yachi and Loreau 1999; Pretzsch and Schütze 2009; Pretzsch et al. 2015b; Riofrío et al. 2016, 2017; Pretzsch and Forrester 2017), (higher) carbon storage capacity (He et al. 2013), ecosystem health and vitality (Jactel et al. 2005, 2009; Balvanera et al. 2006), resistance and resilience (Loreau et al. 2001; Griess et al. 2012), reducing economic risks (Knoke et al. 2008; Griess and Knoke 2013) and for providing insurance against environmental fluctuations (Schütz et al. 2006; Metz et al. 2016; Jactel et al. 2017). However, when the mixture leads to even-aged, mixed-species coniferous stand, the mixture is not necessarily more productive than single-species stands of the component species of the mixture (Chen et al. 2003). In the face of climate change (IPCC 2014), fostering mixed-species forests, with species adapted to various climatic conditions, is considered as one of the most important measures to use in climate-adopted forest management of many forests in Europe (Bolte et al. 2009; Brang et al. 2014). In spite of the lack of the common forest policy in the EU (Dobšinská et al. 2015), diversity of tree species was one of the quantitative indicators of sustainable forest management in Europe adopted by 7th Ministerial Conference in Madrid (SFM 2015). Furthermore, heterogeneity of species composition belongs to ecological attributes which make forests a complex adaptive system (Puettmann et al. 2013; Bauhus et al. 2013). However, despite the important benefits described above, managing mixed forests can be more complex than managing monocultures because of the need to optimize the provision of multiple benefits according to the societal demands (Corona 2014) including sustaining biodiversity and ecosystem functioning (Dieler et al. 2017).

Currently, about 70% of the forest land in Europe is covered by stands composed of two or more tree species (FOREST EUROPE 2015), and a considerable number of former monocultures are undergoing conversion towards more diverse structures. The reasons for conversion and the methods used differ on the basis of geographical and local situations (O'Hara 2001).

A range of silvicultural systems have been proposed to develop mixed-species stands, many of which are associated with the ideas of close-to-nature forestry or systemic forestry (Schütz 1999; Jacobsen 2001; Gamborg and Larsen 2003; Brang 2005; Mlinšek 2006; Bauhus et al. 2013; Brang et al. 2014; Puettmann et al. 2015; O'Hara 2016; Nocentini et al. 2017). Therefore, the effective implementation of these silvicultural systems requires knowledge of the ecology of mixed forests and an understanding of their role in different forest ecosystems. To date, studies have concentrated on different mixtures of species, management practices and specific growing conditions. One of the most important attempts to summarize knowledge about silviculture and management of mixed-species forests in Europe was the book by Olsthoorn et al. (1999). Lately, Pretzsch et al. (2017) have raised issues related to the processes undergoing in mixed-species forests and presented the problems of their modelling, stability, silviculture options and economics. Consequently, the knowledge gained is local, and a wider perspective on sustainable management of mixed forests has yet to be developed (Bravo-Oviedo et al. 2014).

Within the framework of the EuMIXFOR COST Action (http://www.mixedforests.eu), the opportunity came to gather information on the state of the art of current silvicultural approaches used in mixed-species forests in the wide range of countries by biogeographical region (http://www.eea.europa.eu/publications/report_2002_0524_154909) in Europe (Fig. 6.1) and also in the non-European participating countries in the Action. This chapter is going to address the following questions: (1) What are the main mixed tree species combinations found in each participating country and how does this vary by biogeographical region? (2) What are the main management objectives for those mixtures? (3) What silvicultural approaches (regeneration methods, intermediate treatments) are available for the particular mixed-species forests? (4) What are the main challenges (constraints) experienced in mixed tree species forest management?

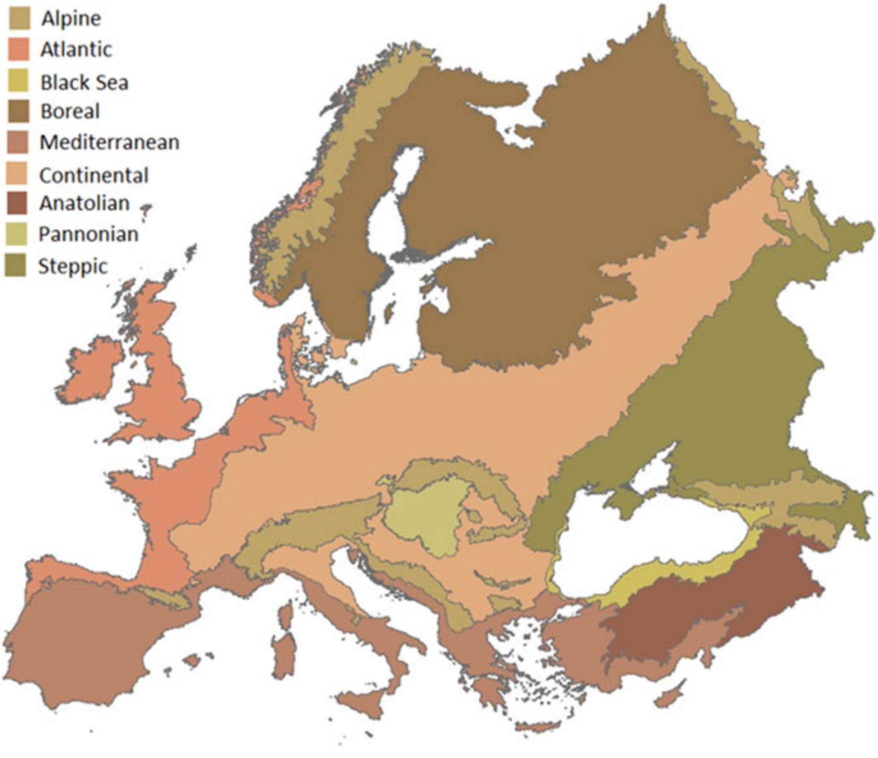

Fig. 6.1 Biogeographical regions in Europe

6.2 Material and Methods

A questionnaire was developed to characterize the silviculture of mixed forests in the participating countries. The two most important and well-described species mixtures were to be selected by biogeographical region (BR) of Europe in each country. 'Most important' means the most widely distributed tree species mixture, whereas 'well-described' refers to the knowledge of the silvicultural treatments and forest management practised in these mixed forest types. We decided to focus on only two types of mixtures because of the difficulty of collecting information about all mixture types in Europe and the impossibility to synthesize such a large range of data. For countries outside Europe, the selection of the mixtures was performed regardless of the biogeographical regions known from Europe. The questionnaire was divided into four main sections: (1) general information on mixture types, (2) management aims and silvicultural treatments, (3) challenges and (4) conversion processes.

The first section presented data on the two types of the most common mixture by biogeographical region and by country. Required information included the criteria applied to define the mixture (volume, stem number, canopy cover, biomass) and the mixed tree species forest types with the dominant species reported first followed by the dominated species. The second section compiled the description of silvicultural practices for the selected mixtures, including the management objectives in order of descending priority; the regeneration methods (vegetative or generative), natural or artificial by seeding or planting; the duration of regeneration period; the silvicultural system (terminology followed Matthews 1991); and the tending operations like weeding, brushing, liberation, precommercial (cleaning) and commercial thinning (methods – from above, from below, mechanical, selection, selective, free style, final crop thinning; intensity as a percentage of the removed growing stock and frequency). Other intermediate treatments like pruning, fertilization, salvage and sanitation cutting and potential for tree species diversification were indicated. The third section was focused on the barriers and gaps in knowledge regarding mixed forests' silviculture, and required improvements were presented. Finally, the last section collected information on conversion processes from pure stands towards mixed forests, but they will not be considered in the chapter.

The questionnaire was sent to 40 countries (30 European, 4 near neighbour and 6 international partner ones), participating in COST Action, and replies were received from 23 European and 4 non-European ones (Algeria, Argentina, Chile, Morocco). Among the national respondents were mostly scientists dealing with silviculture and working at universities or forest research institutes.

The qualitative analysis of the questionnaire was conducted by using the expert judgment of the respondent and the research team in charge of the analysis. The analysis is presented by biogeographical region to facilitate the comparison of silvicultural regimes for the same, or similar, mixtures in different countries within the same biogeographical region (BR). The regions less represented were grouped (Anatolian, Pannonian and Steppic, Sect. 6.3.7). The countries outside Europe were analysed in a separate group (see Sect. 6.3.8). The analysis covers the management objectives pursued, the description of silvicultural treatments and the management challenges according to the respondents. To facilitate the analysis, some generalizations were required. For simplicity reasons, most of the results are presented in a tabular form with the tables covering sections 1–3 of the questionnaire: (1) the type of mixture and its management objective, (2) the silvicultural prescription describing the practices and (3) the management challenges.

6.3 Results

6.3.1 Alpine Biogeographical Region

6.3.1.1 Mixture Types and Management Objectives

The Alpine BR was represented by 11 countries (Fig. 6.2). The most widespread species forming mixtures in the Alpine BR are *Abies alba*, *Fagus sylvatica* and *Picea abies*, whose shares in mixed stands differ significantly between countries (Fig. 6.3). Additionally, other species like *Larix decidua*, *Pinus cembra* and *Pinus mugo* are

Fig. 6.2 Countries in the Alpine BR participating in the survey (*AT* Austria, *BA* Bosnia and Hercegovina, *BG* Bulgaria, *HR* Croatia, *DE* Germany, *IT* Italy, *PL* Poland, *RS* Serbia, *SK* Slovakia, *ES* Spain, *UA* Ukraine)

Fig. 6.3 *Abies alba* Mill.-*Fagus sylvatica* L. mixed forest in the Alpine BR (Southwest Bulgaria) (Source: T. Zlatanov)

present in mixed mountain forests (Table 6.1). In six countries the mixture is defined according to the percentage of tree species in volume, in five countries by canopy cover and in one country by basal area. In 12 mixture types, out of the 21 listed in the Alpine BR, the main management objective is valuable timber (sawtimber) production. For nine of the mixtures, the protection of soils and water or mitigation of erosion or avalanches was indicated as the most important. As a second or third management, objectives were protection (12), timber production (9), biodiversity conservation (7) and recreation and aesthetic (5) (Table 6.1).

6.3.1.2 Silvicultural Prescriptions

The uniform or irregular shelterwood systems are the prevailing regeneration methods in mixed forests of the Alpine BR, usually followed by natural regeneration (Table 6.2). Single tree or group selection systems are the second most widespread applied regeneration method. These systems also rely upon natural regeneration. Shelterwood system was reported for five mixtures. Only in Austria is an individual tree harvesting or clear-cutting system in small areas (up to 0.5 ha) applied. The regeneration period in most countries is rather long and can range from 20 to 60 years. Again only in Austria, the regeneration period is rather short being around 5 years, if planting method is used. Rotation age ranges from 80 in Ukraine to 180 years for *Pinus cembra-Larix decidua* mixture in Italy. Consequently, the target

Table 6.1 Management objectives in the Alpine BR

Mixture type[a]	Country	Management objectives according to the relevance		
		I	II	III
Pa-Fs-Aa[4]	Austria	Valuable timber	Protection (water)	–
Ld-Pa-Pce[4]	Austria	Protection (erosion)	Timber	–
Fs-Aa[2]	Bosnia and Hercegovina	Valuable timber	Protection (soil, water)	–
Fs-Aa-Pa[2]	Bosnia and Hercegovina	Valuable timber	Protection (soil, water)	–
Fs-Aa[2]	Bulgaria	Valuable timber	Protection (water)	Partly recreation/ biodiversity conservation
Pa-Aa[2]	Bulgaria	Valuable timber	Protection (water)	Partly recreation/ biodiversity conservation
Aa-Fs[2]	Croatia	Valuable timber	Protection (soil, water)	–
Aa-Fs-Pa[2]	Croatia	Valuable timber	Protection (soil, water)	–
Pa-Aa,[1] *Fs-Aa,*[1] *Fs-Aa-Pa*[1]	Germany	Valuable timber	Protection (avalanches, rockfall, landslides and water)	Partly recreation/ biodiversity conservation
Pce-Ld[4]	Italy	Protection (soil, water)	Timber production	Biodiversity conservation
Pa-Aa-Fs[4]	Italy	Protection	Timber production	Biodiversity conservation
Aa-Fs[4]	Poland	Protection (soil, water)	Valuable timber	Aesthetics (around spa)
Pa-Aa-Fs[4]	Poland	Protection (soil, water)	Valuable timber	–
Pa-Aa-Fs[2]	Serbia	Protection (soil, water)	Valuable timber	–
Pa-Aa[2]	Serbia	Protection (soil, water)	Valuable timber	–
Pa-Aa-Fs[2]	Slovakia	Valuable timber	Protection (soil, water)	Aesthetics (recreation)
Fs-Aa[2]	Slovakia	Valuable timber	Protection (soil, water)	–
Fs-Aa[4]	Spain	Valuable beech and fir timber	Protection against soil erosion and, natural hazards; aesthetics	Biodiversity
Pa-Aa-Fs[2]	Ukraine	Protection (soil, water)	Valuable timber	–
Fs-Aa-Pa[2]	Ukraine	Protection (soil, water)	Aesthetics	Valuable timber

[a] The mixture was defined according to the percentage of tree species in [1]basal area, [2]volume, [3]stem number and [4]canopy cover

Table 6.2 Silvicultural prescriptions in the Alpine BR

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Pa-Fs-Aa	Austria	CC, IH	NR or AP/5	100–140	Y	CT	Depending on the stage of development	Depending on the stage of development /1–3	SLC, SNC	Y
Ld-Pa-Pc	Austria	IH	NR or AP/20–50	NA	N	NA	NA	NA	SLC	L
Fs-Aa	Bosnia and Hercegovina	SS	NA	NA	NA	NA	NA	NA	SLC, SNC	ND
Fs-Aa-Pa	Bosnia and Hercegovina	SS	NA	NA	NA	NA	NA	NA	SLC, SNC	ND
Fs-Aa	Bulgaria	IS	NR/40–60	120–130/ 50	N	FT	20–25	3	NA	L
Pa-Aa	Bulgaria	IS	NR/30–50	120–130/ 50	N	LT	20–25	3	NA	N
Aa-Fs	Croatia	IS	NR/>20	100/50	Y	CT	20	Depending on the stage of development	SLC, SNC	L
Aa-Fs-Pa	Croatia	IS	NR/>20	100/50	Y	CT	20	Depending on the stage of development	SLC, SNC	L
Pa-Aa, *Fs-Aa*,	Germany	SS, GS	NR/30–60	Around 100/45	Y (if needed)	CT	Depending on the stage	Depending on the stage	SLC	L

(continued)

Table 6.2 (continued)

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Fs-Aa-Pa				(*Pa*,*Aa*); 120–140/ 60(*Fs*)			of development	of development		
Pce-Ld	Italy	IS, GS	NR/≥20	150–180/ 60	NA	FT (SVT)	20–25	Depending on the stand age	NA	N
Pa-Aa	Italy	IS	NR/≥20	120–150/ 60	NA	FT (SVT)	25–30	Depending on the stand age	NA	N
Aa-Fs	Poland	IS	NR/40–50	100/50	Y (W,C)	CT	20	5–7 up to age 60/3–4 than 10/4–5	SLC, SNC	L
Pa-Aa-Fs	Poland	IS	NR/40	100/50	Y (W,C)	CT and LT (*Pa*, >60 years)	20	5–7 up to age 60/3–4 than 10/4–5	SLC, SNC	L
Pa-Aa-Fs	Serbia	SE	NR/NA	NA	NA	NA	NA	NA	SLC, SNC	L
Pa-Aa	Serbia	SE	NR/NA	NA	NA	NA	NA	NA	SLC, SNC	L
Pa-Aa-Fs	Slovakia	SH	NR/30–40	90–120/ 50	Y (C)	CT	15–20	7–10/5–7 (usually 1 per 10 years)	SLC, SNC	Y
Aa-Fs	Slovakia	SH	NR/30–40	100–120/ 50	Y (C)	CT	15–20	7–10/5–7 (usually 1 per 10 years)	SLC, SNC	Y

Fs-Aa	Spain	SH/SS	NR/20–30	120–150/ 45	NA	CT	30	Depending on the stage of development	SNC	L
Pa-Aa-Fs	Ukraine	SH	NR/≥20	80–100/ 30–35	Y (W,C)	CT, IT, LT (depending on age)	15–25	5–7–10–15/ 1–3	SLC, SNC	Y
Fs-Aa-Pa	Ukraine	SH	NR/≥20	100–120/ 40	Y (W,C)	CT, IT, LT (depending on age)	15–35	4–7–10–15/ 1–3	SLC, SNC	Y

diameter at breast height (DBH) is set from 30–35 to 50–60 cm in most mixtures and countries. Release treatments are applied in 11 mixtures, and mostly they involve weeding and cleaning. In most cases thinning from above is used, and 15–25% of growing stock is removed in each intervention. The frequency and number of interventions mostly depend on the development stage of the stand. In some mixtures, the period between interventions ranges from 5 years in younger stands to 15 years in older ones. Salvage and sanitation cuttings are performed almost in all mixtures. In the case of the selection system, there is no regeneration period, rotation age, release treatments or thinning. For about half of the listed mixtures, limited potential for tree species diversification was indicated. However, for mixtures growing in relatively harsh climatic conditions (Italy, Bulgaria), the potential for tree species diversification is not considered. Only Slovakia and Ukraine identified possibilities to enrich species composition.

6.3.1.3 Challenges of Management

The most common challenge of management of mixed-species stands in the Alpine region is a high browsing pressure from ungulates and other animals which was indicated in eight mixtures, including six cases on the first place (Table 6.3). Climate change impact was identified as almost important as game pressure, but mostly as a second or further factor. Problems with European silver fir in mixed stands (decline, growing in mixture, regeneration) and the loss of selection structure were also often mentioned. In some mixtures, very important challenges are prevention against pest and disease attack, regeneration, growing and wind damages of *Picea abies* and gaps of knowledge in effective ways of regeneration. Another group of factors influencing management includes steep terrain, poor road infrastructure, difficult and dangerous access because of wartime minefields and insufficient education of forest managers.

6.3.2 Atlantic Biogeographical Region

6.3.2.1 Mixture Types and Management Objectives

Six countries belonging to the Atlantic BR responded to the survey (Fig. 6.4). The Atlantic region is very diverse in terms of most important mixed forest species composition (Table 6.4). Mixtures are mainly dominated by coniferous species (*Pinus sylvestris*, *Picea abies*, *Picea sitchensis*, *Abies alba*, *Pseudotsuga menziesii*, *Pinus contorta*, *Larix* spp.), but also broadleaved species like *Fagus sylvatica*, *Quercus robur*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Betula pendula* and *Quercus petraea* are very important (Fig. 6.5). More mixtures (six) are defined according to the species share of the basal area than by stem numbers (four types in Great Britain and Ireland).

Table 6.3 Challenges of management in the Alpine BR

Mixture type	Country	Challenges according to the relevance				
		I	II	III	IV	V
Pa-Fs-Aa	Austria	Steep terrain	High game pressure	Taming beech regeneration	–	–
Ld-Pa-Pc	Austria	Steep terrain	High game pressure	–	–	–
Fs-Aa	Bosnia and Hercegovina	Losing selection structure	The residue after the war (mines)	Poor road infrastructure	Climate change impacts	Education of forest managers
Fs-Aa-Pa	Bosnia and Hercegovina	Losing selection structure	Phytosanitary problems of spruce	Poor road infrastructure	Climate change impacts	Education of forest managers
Fs-Aa	Bulgaria	Climate change impacts	Education of forest managers	–	–	–
Pa-Aa	Bulgaria	Climate change impacts	Prevention of pest and disease attack	Education of forest managers	–	–
Aa-Fs	Croatia	*Aa* decline	Losing selection structure	The residue after the war (mines)	Poor road infrastructure	Climate change impacts
Aa-Fs-Pa	Croatia	*Aa* decline	Losing selection structure	The residue after the war (mines)	Poor road infrastructure	Climate change impacts
Fs-Aa, *Fs-Aa-Pa*, *Pa-Aa*	Germany	High ungulate pressure	Soil degradation because of past over-use	Gaps in knowledge in effective ways of regeneration	–	–
Pce-Ld	Italy	High elevation and steep slopes make management very difficult	Regeneration system considering the ecological preferences of the two species	–	–	–

(continued)

Table 6.3 (continued)

Mixture type	Country	Challenges according to the relevance				
		I	II	III	IV	V
Pa-*Aa*	Italy	Relatively high ungulate pressure, management system ensuring suitable natural regeneration	–	–	–	–
Aa-*Fs*	Poland	High game pressure	Difficulties to obtain natural regeneration of *Aa* beneath the canopy of *Aa*	Spring ground frost (beech)	–	–
Pa-*Aa*-*Fs*	Poland	High game pressure	Difficulties to obtain natural regeneration of *Aa* beneath the canopy of *Aa*	Spring ground frost (*Fs*)	Wind damages among spruce	–
Pa-*Aa*-*Fs*	Serbia	Prevention of pest and disease attack	Gaps in knowledge in effective ways of regeneration	Climate change impacts	–	–
Pa-*Aa*	Serbia	Prevention of pest and disease attack	Losing selection structure	Climate change impacts	–	–
Pa-*Aa*-*Fs*	Slovakia	High ungulate pressure (esp. conifers)	Dieback of *Pa*	–	–	–
Fs-*Aa*	Slovakia	High ungulate pressure (esp. conifers)	–	–	–	–
Fs-*Aa*	Spain	Phytosanitary problems of fir	More knowledge about fir decay and possible interactions with other species is needed	Climate change impact	–	–
Pa-*Aa*-*Fs*	Ukraine	Preservation of natural regeneration during harvesting	Lack of care for plants at a young age	Reduction of soil fertility because of water erosion	Education of forest managers	–
Fs-*Aa*-*Pa*	Ukraine	Lack of natural regeneration of *Pa* under the canopy of mature plants	Loss of natural beech regeneration due to the intensive development of grass and damage by frost	Development of model of mixed stands	Planting spruce after felling and tending treatment	Education of forest managers

Fig. 6.4 Countries in the Atlantic BR participating in the survey (*BE* Belgium, *DK* Denmark, *DE* Germany, *GB* Great Britain, *IE* Ireland, *ES* Spain)

The most important management objective, in the first place according to relevance, in almost all listed mixtures is valuable timber (sawtimber) production, except for *Quercus robur*/*Quercus petrae*-*Betula pendula*/*Betula pubescens* mixture in Great Britain, where restoration of native woodlands is the predominant aim followed by biodiversity, production of valuable timber and firewood and landscape. Other aims like biodiversity, water protection, wildlife (game) habitat, recreation, property value, protection against soil erosion, natural hazards and aesthetics, multifunctionality and nursing of oak by pine and of beech by conifers are listed as lesser important ones.

6.3.2.2 Silvicultural Prescriptions

Various regeneration methods used in Atlantic BR are a reflection of the variability of species combinations in the region (Table 6.5). The methods range from clear-cutting in Denmark and Ireland, through patch clear felling and uniform and irregular shelterwood system, up to single tree and group selection system in Germany, Belgium and Denmark as well if possible. Both natural regeneration and planting occur with regeneration periods of up to 20 years or even longer to 30–40 in

Table 6.4 Management objectives in the Atlantic BR

Mixture type^{a}	Country	Silvicultural objective according to the relevance				
		I	II	III	IV	V
Fs-Qr^{1}	Belgium	Valuable beech and oak timber	Multifunctionality	–	–	–
Qr-Aps-Fe^{1}		Valuable beech, maple, ash and oak timber				
Psy-Qr-Bpe^{1}	Belgium	Valuable pine, oak and birch timber	–	–	–	–
Psi-Aa^{1}	Denmark	Profitable timber production	Wildlife (game) habitat	Recreational purposes	Protection of soil	–
Pa-Pm^{1}	Denmark	Profitable timber production	Wildlife (game) habitat	Property value	Recreational purposes	Protection of soil
Fs-Pa^{1}	Germany	Valuable timber and fuelwood	Biodiversity	Partly drinking water protection	Recreation	–
Psi-Psy (Pco/Lspp)^{3}	Great Britain	Production of sawtimber along with pulp and chipwood	–	–	–	–
Qr(Qp)-Bpe(Bpu)^{3}	Great Britain	Restoration of native woodlands	Biodiversity	Production of valuable timber (lowland Britain)	Timber production and firewood (in upland Britain)	Landscape (in lowland Britain)
Qr-Psy(Ld)^{3}	Ireland	Valuable oak and pine timber	Nursing of the oak by the pine	–	–	–
Fs-Psy(Ld)^{3}	Ireland	Valuable beech timber and intermediate conifer timber	Nursing of beech by the conifer	–	–	–
Psy-Fs^{1}	Spain	Valuable beech and pine timber	Protection against soil erosion and natural hazards; aesthetics	Biodiversity	–	–

[a] The mixture was defined according to the percentage of tree species in ^{1}basal area, ^{2}volume, ^{3}stem number and ^{4}canopy cover

Fig. 6.5 *Fagus sylvatica* L.-*Quercus robur* L. mixed forest in the Atlantic BR (Southern Germany) (Source: Ch. Ammer)

Germany. Rotation age and target DBH depend mostly on tree species and site conditions. In all mixtures, release treatments are applied through weeding or cleaning in a few cases. Thinning from above and final crop tree thinning are dominant methods of treatments. In some mixtures thinning from below or selective thinning is performed. The intensity of thinning is at the most removal of 30% of growing stock with frequency ranging from 3 to 15 years depending on the stage of stand development. In Belgium, Denmark and Ireland (broadleaf), artificial pruning is applied to increase timber quality. In other countries, salvage and sanitation cuttings are used to improve stand condition. The potential for tree species diversification is indicated for most of the mixtures.

6.3.2.3 Challenges of Management

The lack of management rules for mixtures was considered the most significant challenge, reported as the primary challenge for five types (Table 6.6). The second most important challenge is high game pressure. Less common challenges are improved growth and yield models for mixed stands and low interest of owners in forest management. Other issues vary according to mixture species composition and are mostly indicated only once.

Table 6.5 Silvicultural prescriptions in the Atlantic BR

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Fs-Qr	Belgium	GS	AP, NR/10	100–120(*Fs*)/60 120(*Qr*)/60 100(*Ap*)/50 100(*Fe*)/50	Y	CRT	ND	5–10/5–10	PR	ND
Qr-Ap-Fe										
Psy-Qr-Bpe	Belgium	SH	NR (AP)/5	60(*Bpe*)/50 100(*Psy*)/50 120(*Qr*)/60	Y	CRT	ND	5–10/5–10	PR	ND
Psi-Aa	Denmark	CC, SH, IS or GS	NR, AP/1–20	35–50(*Psi*), 60–100(*Aa*)/ 35–40(*Psi*), 50–60(*Aa*)	Y	CT later SVT or NO (*Psi*) and SVT (*Aa*)	10–15	3–10/5–8	SLC, SNC	Y
Pa-Pm	Denmark	CC, SH, IS or GS	NR, AP/1–20	40–80 (*Pa*) 60–100 (*Pm*)/ 35–40(*Pa*), 50–90(*Pm*)	Y	CT later SVT	15	3–10/5–8	PR, SLV SNC	Y
Fs-Pa	Germany	SS, GS	NR/30–40	80/45(*Pa*); 120/60(*Fs*)	Y (if needed)	CT	Depending on the stage of development	Depending on the stage of development// 1 per 10 years	SLC	Y

Psi-Psy (Pc/Lspp)	Great Britain	PCF	AP/–	40–60/30–50	Y (W,C)	LT	20	5/2	NA	L
Qr(Qp)-Bpe(Bpu)	Great Britain	PCF, CS, IS, GS	NR (AP)/ 5–10	100–150/60–80	Y (W,C)	CT (IT)	15–20	10–15/4–7	NA	Y
Qr-Psy (Ld)	Ireland	CC	AP (NR)/–	[a]	Y (W)	CRT	50–100(*Psy*) 0–30(*Qr*)	Depending on the stage of development	PR	ND
Fs-Psy (Ld)	Ireland	CC	AP (NR)/–	[a]	Y (W)	CRT	50–100(*Psy*) 0–30(*Fs*)	Depending on the stage of development	PR	ND
Psy-Fs	Spain	SH	NR/≥20	120–130	Y (if needed)	LT/CT in some areas	20–30	Depending on the stage of development	SLC, SNC	L

[a] Plantations are too young to determine

Table 6.6 Challenges of management in the Atlantic BR

Mixture type	Country	Challenges according to the relevance			
		I	II	III	IV
Fs-Qr	Belgium	Lack of management rules for mixtures	Low timber quality of the broadleaved species	–	–
Qr-Ap-Fe					
Psy-Qr-Bpe	Belgium	Lack of management rules for mixtures	–	–	–
Psi-Aa	Denmark	High game pressure (*Aa*)	Windfall and bark beetle (*Psi*)	–	–
Pa-Pm	Denmark	Frost damage (*Pm*)	Inter-tree competition	High game pressure (*Pm*)	–
Fs-Pa	Germany	Unknown behaviour of tree species response to climate change	High browsing pressure	Regionally high N-inputs from agriculture	–
Psi-Psy (Pc/Lspp)	Great Britain	Duration of nurse tree keeping in mixtures	Improved growth and yield models for mixed stands	Long-term impacts of 'nursing' mixtures on timber properties of spruce	Integrating the mixture effect into decision support tools that are used to guide species choice under a climate change scenario
Qr(Qp)-Bpe(Bpu)	Great Britain (both types)	Devising cost-effective methods for the control of animal browsing	Achieving adequate natural regeneration of the species to be used in mixture	Appropriate thinning regimes for use in mixtures	Improved growth and yield models for mixed stands
Qr-Psy (Ld)	Ireland	Knowledge how to grow mixtures	Low interest of owners in forest management	–	–
Fs-Psy (Ld)	Ireland	Knowledge how to grow mixtures	Low interest of owners in forest management	–	–
Psy-Fs	Spain	Knowledge how to grow mixtures	–	–	–

6.3.3 Black Sea Biogeographical Region

6.3.3.1 Mixture Types and Management Objectives

The Black Sea BR is represented only by two countries (Fig. 6.6) with four types of mixed-species stands (Table 6.7). Oaks (*Quercus frainetto*, *Quercus cerris*, *Quercus petraea*) are the main tree species in Bulgaria, while in Turkey species composition is more varied (Fig. 6.7). In mixed stands consisting of oaks (Bulgaria), species proportion is based on their share in volume, whereas in mixed stands in Turkey, this is based on canopy cover. The most significant management objective is valuable timber production followed by firewood production and protection (soil).

Fig. 6.6 Countries in the Black Sea BR participating in the survey (*BG* Bulgaria, *TR* Turkey)

Table 6.7 Management objectives in the Black Sea BR

Mixture type[a]	Country	Silvicultural objective according to the relevance	
		I	II
Qfr-Qce[2]	Bulgaria	Firewood	Protection (soil)
Qp-Qrf[2]	Bulgaria	Valuable timber production	Protection (soil)
Fot-Cs(Tspp/Caspp/Aspp)[4], *Fot-An*[4]	Turkey	Valuable timber production	–

[a] The mixture was defined according to the percentage of tree species in [1] basal area, [2] volume, [3] stem number and [4] canopy cover

Fig. 6.7 *Carpinus betulus* L.-*Tilia rubra* and *T. tomentosa* Moench-*Acer campestre* L.-*Acer platonoides* L.-*Cestanea sativa* Mill. mixed forest in Black Sea BR (Duzce, the north-western region of Turkey) (Source: O. Yildiz)

6.3.3.2 Silvicultural Prescriptions

The irregular shelterwood system prevails in the oak forests in Bulgaria (Table 6.8). The mixed stands of Turkey are managed by clear-cutting or single tree selection system followed by natural generative or vegetative regeneration with up to 30 years of regeneration period (Bulgaria). Rotation age ranges between 80 and 100 years. Only in Turkey release treatments in the form of cleaning or liberation are performed. Intermediate, low or free style of thinning is applied with 20–25% of intensity. In Turkey salvage and sanitation cuttings are performed. The mixtures are considered to have the potential for tree species diversification.

Table 6.8 Silvicultural prescriptions in the Black Sea BR

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Qf-Qc	Bulgaria	IS	NR, VR/30	80/ND	N	LT or FT	20–25	2	NA	Y
Qp-Qfr	Bulgaria	IS	NR, VR/30	80/ND	N	LT or FT	20–25	2–3	NA	Y
Fot-Csa (Tspp/ Cspp/ Aspp)	Turkey	CC with seed trees	NR/NA	80/ND	Y (C)	IT	20–25	2	SLC, SNC if needed	Y
Fot-An	Turkey	SS	NR/NA	100(*Fot*, *An*)/55 (*Fot*), 50 (*An*)	Y (C,L)	IT (*Fot*)/ SVT (*An*)	20–25	2	SLC, SNC if needed	Y

Table 6.9 Challenges of management in the Black Sea BR

Mixture type	Country	Challenges according to the relevance	
		I	II
Qf-Qc	Bulgaria	Decreased vitality at some places due to many rotations of coppice management	Lack of successful transformation to seed-originated stands due to insufficient care of newly regenerated seedlings
Qp-Qfr	Bulgaria	Decreased vitality at some places due to many rotations of coppice management	Lack of successful transformation to seed-originated stands due to insufficient care of newly regenerated seedlings
Fot-Csa (Tspp/Cspp/Aspp)	Turkey	Management focuses on other objectives (e.g. diversity)	Lack of information on the growing different mixtures
Fot-An	Turkey	Management focuses on other objectives (e.g. diversity)	Lack of information on the growing different mixtures

6.3.3.3 Challenges of Management

Since mixed oak stands in Bulgaria are very often derived from vegetative reproduction, decreasing vitality of some stands is observed due to many rotations of coppice management (Table 6.9). In Turkey, the management of the mixtures should be focused not only on valuable timber production but also on maintaining and enhancing tree species diversity. Other challenges are the lack of successful transformation to seed-originated stands due to the insufficient care of newly regenerated seedlings (Bulgaria) and lack of information on the growing of different mixtures (Turkey).

6.3.4 Boreal Biogeographical Region

6.3.4.1 Mixture Types and Management Objectives

Four countries from the Boreal BR responded to the survey (Fig. 6.8). In Northern Europe where the Boreal BR dominates, the main tree species are *Pinus sylvestris*, *Picea abies* and *Betula pendula* (Fig. 6.9) which are growing either in pure stands or in various mixture combinations (Table 6.10). The share of each species in stand composition is mainly based on a percentage of volume or basal area (only Estonia). The predominant management aim is the production of valuable *Pinus sylvestris*, *Picea abies* and also *Betula pendula* timber. Additional important aims in mixtures of Estonia are sustainable bioeconomy and sustainable forest ecosystems, biodiversity and resilience with habitat and species protection. In Sweden, the management is focused also on volume (more on quantity, less on quality of timber) production, nature (habitat and species) protection and recreation. The last mentioned objective is also of importance in Lithuania.

Fig. 6.8 Countries in the Boreal BR participating in the survey (*EE* Estonia, *LV* Latvia, *LT* Lithuania, *SE* Sweden)

Fig. 6.9 *Pinus sylvestris* L.-*Picea abies* (L.) Karst mixture forest in the Boreal BR (Latvia) (Source: Z. Libiete-Zalite)

Table 6.10 Management objectives in the Boreal BR

Mixture type[a]	Country	Silvicultural objective according to the relevance	
		I	II
Psy-Bpe[1]	Estonia	Sustainable bioeconomy – valuable pine and birch timber	Sustainable forest ecosystems biodiversity and resilience – habitat and species protection
Pa-Bpe[1]	Estonia	Sustainable bioeconomy – valuable spruce and birch timber	Sustainable forest ecosystems biodiversity and resilience – habitat and species protection
Pa-Bspp[2]	Latvia	High-quality pine and spruce sawlogs, veneer logs	–
Psy-Pa[2]	Latvia	High-quality pine and spruce sawlogs	–
Psy-Pa[2]	Lithuania	Valuable timber production	Recreation
Pa-Bpe[2]	Lithuania	Valuable timber production	–
Pa-Psy[2]	Sweden	Volume production (spruce), valuable timber production (pine)	Recreation
Pa-Bpe[2]	Sweden	Volume production	Nature protection – habitat and species protection

[a]The mixture was defined according to the percentage of tree species in [1]basal area, [2]volume, [3]stem number and [4]canopy cover

6.3.4.2 Silvicultural Prescriptions

The main regeneration method adopted in the region is the clear-cutting system followed by artificial regeneration (Table 6.11). Usually, the main species (*Pinus sylvestris*, *Picea abies*) are planted, but sometimes seeding is also used if possible after the cutting, while *Betula pendula* is naturally regenerated. In the case of natural regeneration, the regeneration period is very short (1–10 years). The rotation age ranges from 70 to 120 years (*Pinus sylvestris*, *Picea abies*) and 40–70 (*Betula pendula*) with target DBHs varying between 27 and 40 cm (*Pinus sylvestris*, *Picea abies*) and 16–31 cm (*Betula pendula*). In Swedish mixtures, the target DBH of *Pinus sylvestris* and *Picea abies* is larger (30–40 cm) than in other countries in the region and depends on site conditions. In all mixtures, release treatments in the form of cleaning or weeding are applied. The most widespread thinning methods in the listed mixed stands are from below and from above followed by intermediate and free style of thinning. The intensity of thinning in four mixtures (Latvia, Sweden) is variable and in the other four does not exceed 20 (Estonia) or 25% (Lithuania). The frequency of thinning in Latvia depends on stand basal area, whereas in other countries, it ranges between 5 and 20 years. Salvage or sanitation cuttings are the main other treatments applied in almost all mixtures. Pruning is usual in Estonia and Latvia with the aim of obtaining valuable timber production. In Sweden fertilization is used as another effective treatment.

6.3.4.3 Challenges of Management

Among the most important challenges identified (Table 6.12) are high game pressure (Sweden) and limited management pathways for one stand in one rotation (Estonia). Next significant issues of mixed forest management listed first are too high rotation

Table 6.11 Silvicultural prescriptions in the Boreal BR

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Psy-Bpe	Estonia	CC	AS, AP, NR/ 5–10	90–120(*Psy*), 60–70(*Bpe*)/ 28(*Psy*), 16–26(*Bpe*)	Y (C)	CT, LT, FT	20	10–20/1–3	PR, SLC, SNC	Y
Pa-Bpe	Estonia	CC	AS, AP, NR/ 5–10	90–120(*Pa*), 60–70(*Bpe*)/ 28(*Pa*), 16–26(*Bpe*)	Y (C)	CT, LT, FT	20	10–15/1–2	PR, SLC, SNC	L
Psy-Pa	Latvia	CC	AP(*Psy*,*Pa*), NR(*Pa*)/5	101(*Psy*), 81 (*Pa*)/27–39 (*Psy*), 27–31 (*Pa*)	Y (W)	LT	Various	Depending on stand basal area	PR, SNC	L
Pa-Bspp	Latvia	CC	AP(*Pa*), NR (*Pa*), NR (*Bspp*)/5	81(*Pa*), 71 (*Bspp*)/27–31 (*Pa*), 22–31 (*Bspp*)	Y (W)	LT	Various	Depending on stand basal area	PR, SNC	L
Psy-Pa	Lithuania	CC	AP/3	101(*Psy*), 71 (*Pa*)/NA	Y (C)	CT, IT	10–25	5–15/3–4	SNC	Y
Pa-Bpe	Lithuania	CC	AP(*Pa*), NR (*Bpe*)/3	71(*Pa*), 61 (*Bpe*)/NA	Y (C)	CT, IT	10–25	5–10/4–5	SNC	Y
Pa-Psy	Sweden	CC	AP, NR/1–5	70–120/ (30–40 if any)	Y	LT (CT)	Various	15/1–5	SLC, FE	L
Pa-Bpe	Sweden	CC	AP, NR/1–10	70–120(*Pa*), 40(*Bpe*)/30 (*Pa*)	Y	LT (CT)	Various	10/1–3	SLC	L

Table 6.12 Challenges of management in the Boreal BR

Mixture type	Country	Challenges according to the relevance		
		I	II	III
Psy-Bpe	Estonia	Limited management pathways for one stand in one rotation	Lack of information on growing different mixtures	Lack of management models for mixtures
Pa-Bpe	Estonia	Limited management pathways for one stand in one rotation due to high rotation age for spruce	Lack of information on growing different mixtures	Lack of management models for mixtures
Psy-Pa	Latvia	Too high rotation age for spruce	Root rot (*Pa*)	–
Pa-Bpe	Latvia	Conflicting composition	Root rot (*Pa*)	Incorrect estimation of standing spruce volume (second storey) affecting decision making
Psy-Pa	Lithuania	Problems to get natural regeneration of *Psy*	Game pressure on *Psy*	*Ips typographus* damage
Psy-Bpe	Lithuania	*Pa* must be planted in clear-cuts and later promoted by thinnings	*Bpe* often compete with less valuable *Populus tremula* and *Alnus incana*	*Ips typographus* damage
Pa-Psy	Sweden	High game pressure	Gaps in knowledge of interactions between browsers and plants	Education of forest managers
Pa-Bpe	Sweden	High game pressure	Gaps in knowledge of interactions between browsers and plants	Education of forest managers

age for spruce and conflicting composition (Latvia), problems to get natural regeneration of *Pinus sylvestris* and promotion of artificial regeneration of *Picea abies* (Lithuania). Other challenges of lesser priority (pointed out in two mixtures) are gaps in knowledge of interactions between browsers and plants, lack of management models for mixtures, *Ips typographus* damages and education of forest managers.

6.3.5 Continental Biogeographical Region (BR)

6.3.5.1 Mixture Types and Management Objectives

The number of countries belonging to the Continental BR that replied to the survey was as big as in the case of the Alpine BR (Fig. 6.10). Mixed forests in the Continental BR are mainly dominated by broadleaved (*Quercus*, *Fagus*, *Fraxinus*,

Fig. 6.10 Countries in the Continental BR participating in the survey (*AT* Austria, *BE* Belgium, *BG* Bulgaria, *CZ* Czech Republic, *DK* Denmark, *HR* Croatia, *DE* Germany, *IT* Italy, *PL* Poland, *RS* Serbia, *UA* Ukraine)

Carpinus, *Tilia*, *Acer*) and coniferous tree species (*Pinus sylvestris*, *Picea abies*) (Table 6.13, Fig. 6.11). The species share in the mixtures is based on the percentage of volume (nine mixtures), canopy cover (seven) and basal area (six).

The silvicultural objectives are very diverse. Valuable timber production, which is indicated in 14 mixtures as the main objective, is common in this region followed by the protection of soil, water and biodiversity (which is the main goal in five types). Firewood production is reported by Bulgaria and Serbia. Recreation, landscape and other social functions are important management aims in the Czech Republic, Denmark and Italy. One of the significant management aims of two mixtures in Denmark is the creation of wildlife (game) habitat. Other goals like multifunctionality, hunting, fuelwood production, property value, protection of groundwater, non-wood forest products and conversion to high forest were mentioned by respondents only once.

Table 6.13 Management objectives in the Continental BR

Mixture type[a]	Country	Silvicultural objective according to the relevance				
		I	II	III	IV	V
Pa-Fs^{4}	Austria	Valuable timber	Protection (water)	–	–	–
Psy-Pa^{4}	Austria	Valuable timber	–	–	–	–
Fs-Qp(Qr)^{1}	Belgium	Valuable beech and oak timber	Multifunctionality	–	–	–
Fs-Aps-Fe-Qr^{1}		Valuable beech, maple, ash and oak				
Pm-Pa^{1}	Belgium	Valuable timber	–	–	–	–
Qp-Qce^{2}	Bulgaria	Firewood	Protection (soil)	–	–	–
Qr-Cb^{2}	Croatia	Valuable oak timber	–	–	–	–
Qp-Cb^{2}	Croatia	Valuable oak timber	–	–	–	–
Psy-Qp-Cb-Tc^{2}	The Czech Republic	Valuable timber production	Aesthetics in special purpose forests (recreation, social functions)	Biodiversity	Protection (soil, water)	–
Pa-Fs^{2}	The Czech Republic	Valuable timber production	Protection (soil, water)	Recreation and other social functions	Biodiversity	–
Fs-Aps(Fe)^{1}	Denmark	Wildlife (game) habitat	Profitable timber production	Recreational purposes and landscape aesthetics	Protection of groundwater	Biodiversity
Fe-Ag^{1}	Denmark	Protection of biodiversity	Wildlife (game) habitat	Property value	Recreational purposes and landscape aesthetics	Profitable timber production

Psy-Qr[1]	Germany	Valuable timber	Biodiversity	Partly drinking water protection	Recreation	–
Qr-Cb-Fspp-Um-Aspp[4]	Italy	Biodiversity conservation	Recreation	Timber production	Non-wood forest products	–
Oc-Fon-Qpu[4]	Italy	Protection	Fuelwood production	Biodiversity conservation		
Psy-Qr(Qp)[4]	Poland	Valuable timber production (*Ps*)	Protection (soil, water)	–	–	–
Fs-Qr(Qp)[4]	Poland	Valuable timber production	Protection (soil, water)	–	–	–
Qr-Fa[2]	Serbia	Protection (soil, water)	Valuable timber production	–	–	–
Qce-Qfr[2]	Serbia	Protection (soil, water)	Valuable timber production	Firewood	Conversion to high forests	–
Psy-Qr[2]	Ukraine	Valuable oak and pine timber	–	–	–	–
Qr-Cb[2]	Ukraine	Valuable oak timber	–	–	–	–

[a] The mixture was defined according to the percentage of tree species in [1]basal area, [2]volume, [3]stem number and [4]canopy cover

Fig. 6.11 *Pinus sylvestris* L.-*Quercus petraea* (Matt.) Liebl. mixture forest in the Continental BR (Germany) (Source: L. Steinacker)

6.3.5.2 Silvicultural Prescriptions

A range of regeneration methods is used in the Continental BR (Table 6.14). The most common is the uniform shelterwood system which is used in 13 mixtures followed by clear-cutting (seven mixtures), irregular shelterwood (five mixtures), group selection (four mixtures), single tree selection (one mixture) and coppice-with-standard (one mixture) method. Natural regeneration is the primary method employed in mixtures, but artificial planting, seeding and vegetative reproduction are also applied. The regeneration period ranges from 1 year up to 40 years in the shelterwood method. The rotation age is variable and depends on species and site conditions. The shortest one (25–30 years) refers to *Ostrya carpinifolia-Fraxinus ornus-Quercus pubescens* mixture in Italy regenerated by vegetative reproduction. The second shortest rotation age (60–70 years) is applied to *Pseudotsuga menziesii-Picea abies* mixture in Belgium. The longest one (160–240 years) refers to *Pinus sylvestri-Quercus robur* mixture in Germany. The target diameter depends on tree species and site conditions and ranges from 35–40 cm in *Pinus sylvestris-Quercus robur* mixture (Ukraine) to 80 cm mostly for oak in few mixed types. Release treatments in the form of weeding, cleaning, brushing and liberation are performed in almost all mixtures. Only mixed types in Italy, Bulgaria and one in Belgium are not the subjects of this intervention. The most widespread thinning method is crown thinning (from above) followed by other methods like free, selective, low (from below) and intermediate thinning. The intensity of thinning depends on the stage of stand development in many mixtures. It can reach even 40% of growing stock during

Table 6.14 Silvicultural prescriptions in the Continental BR

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Pa-Fs	Austria	SH or GS	NR or AP/5	90/50	Y (L,W)	FT, SVT	Depending on the stage of development	Depending on the stage of development/4	SLC, SNC	Y
Psy-Pa	Austria	CC or SH	NR or AP/5	90/50	Y (L,W)	FT, SVT	Depending on the stage of development	Depending on the stage of development/4	SLC, SNC	Y
Fs-Qp (Qr)	Belgium	SS, GS	NR/NA	150/80	N	SNT	Around increment	12(3,6,9)/NA	PR, FE	Y
Fs-Aps-Fe-Qr										L
Pm-Pa	Belgium	CC	AP/NA	60–70/50	Y (C)	CT	40 (first thinning) down to 20–25(last entry)	3–6/10	PR	L
Qf-Qc	Bulgaria	IS	NR, VR/30	80/-	N	LT or FT	20–25	2	NA	Y
Qr-Cb	Croatia	SH	NR (AP, AS)/10–20	120/ 70–80	Y (W,B, C)	CT	20–30	1 per 10 year	SLC, SNC	Y
Qp-Cb	Croatia	SH	NR (AP, AS)/10–20	120/ 50–60	Y (W,B, C)	CT	20	1 per 10 year	SLC, SNC	Y
Ps-Qp-Cb-Tc	The Czech Republic	SH	NR, AP/ 20–30	100–130/ 40–50	Y (W,B, C)	CT	≤ 20	3–7/ND	SLC, SNC	ND

(continued)

Table 6.14 (continued)

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Pa-Fs	The Czech Republic	SH	NR, AP/ 30–40	120/ 40–50	Y (W,B, C)	LT (*Pa*), CT	≤15	5–10/ND	SLC, SNC	ND
Fs-Aps (Fe)	Denmark	CC, SH, IS or GS	NR or AP/1–30	80(*Aps*)-120(*Fs*)/ ≥57 (*Fs*), > 47 (*Aps*)	L	CT	10–15	3–15/8–18	ND	Y
Fe-Ag	Denmark	CC, SH, IS or GS,	NR, VR or AP/0–15	ND	L	CT	15–20	3–15/3–20	SLC, SNC	Y
Psy-Qr	Germany	SH	NR/20–30	120/60 (*Psy*); 160–240/ 70(*Qr*)	Y (if needed)	CT	Depending on the stage of development	Depending on the stage of development/1 per 10 years	PR(*Psy*)	Y
Qr-Cb-Fspp-Um-Aspp	Italy	IS	NR/10–30	120/60	NA	CT	20–30	Depending on the stage of development/1 per 15 years	PR	Y
Oc-Fon-Qpu	Italy	CS	VR (NR)/ 10–30	25–30/ ND	NA	NA	NA	NA	NA	Y

Psy-Qr (Qp)	Poland	CC, SH	AP, NR(*Qr*/*Qp*)/11–20	90–110 (*Psy*), 140–160 (*Qr*/*Qp*)/ 50–60 (*Psy*), 60–80 (*Qr*/*Qp*)	Y (W,C)	CT, LT for *Psy*>=60 years	20	5–7 up to age 40 years/3–4 then 8-10/4-8 (*Qr/Qp*)	SLC, SNC	Y
Fs-Qr (Qp)	Poland	SH	NR/10–30	100–120 (*Fs*), 140–160 (*Qr*/*Qp*)/ 60(*Fs*), 60–80 (*Qr*/*Qp*)	Y (W,C)	CT	20–25	5–7 up to age 40 years/3–4 then 8-10/4-8 (*Qr/Qp*)	SLC, SNC	L
Qr-Fa	Serbia	SH	NR/20	120–140/ 60–80	Y (W,C,B, L)	CT	15–20	1 per 10 years	PR, SNC	L
Qc-Qf	Serbia	SH	NR /10–20	80–100/-	Y (W,C,B, L)	CT	15–20	1 per 10 years	PR, SNC	Y
Psy-Qr	Ukraine	CC (IS)	NR, AP/10	80–90/ 35–40	Y (W,B, C)	CT, IT, LT (depending on age)	15–20	5–7–10–15–25/1–2	SLC, SNC, PR, FE	Y
Qr-Cb	Ukraine	CC	AP, AS/10	100–110/ 40–45	Y (W,B, C)	CT, LT (depending on age)	10–15–25–45	5–7–10–20/ 1–2	SNC, FE	Y

the first entry in the mixture *Pseudotsuga menziesii-Picea abies* (Belgium). However, in most mixed types, the intensity is not higher than 25–30% of growing stock. The frequency of thinning also depends on the stage of stand development and amounts from 3 to 7 years in younger stands up to 15 or even 25 (Ukraine) years in older mixtures. Other intermediate treatments like salvage and sanitation cuttings are performed in almost all mixtures. In Belgium, Germany, Italy, Serbia and Ukraine, artificial pruning is applied in order to achieve better timber quality. Fertilization is indicated in the case of three mixtures, one in Belgium and two in Ukraine. The potential for tree species diversification is considered to exist or to be limited in almost all mixtures.

6.3.5.3 Challenges of Management

The challenges indicated by respondents in questionnaires are very variable, and there is no single one that dominates (Table 6.15). The most common challenges listed in the first ranked column are (1) obtaining and maintaining natural regeneration, especially of *Quercus robur*, which is threatened by other expansive tree species (*Carpinus*, *Fagus*), (2) steep terrain making forest operations difficult, (3) lack of management rules and models for mixtures and (4) high game pressure. The remaining challenges listed in Table 6.15 occur once or twice at the most, and they are so different that it is difficult to aggregate them.

6.3.6 Mediterranean Biogeographical Region

6.3.6.1 Mixture Types and Management Objectives

Seven countries (Fig. 6.12) laying in the Mediterranean BR provided information in the questionnaire. Mixed tree species configurations occurring in the Mediterranean BR are mostly composed of *Quercus*, *Pinus* and *Carpinus* species and to a lesser extent *Fagus*, *Abies*, *Cedrus*, *Fraxinus*, *Castanea* and others (Table 6.16, Figs. 6.13). The share of each listed species in the mixtures is based on the percentage of canopy cover in most cases. Only in Bosnia and Hercegovina mixtures are characterized by species share in volume. The most important silvicultural objective in this region is the protection of soil and water (five mixtures) followed by valuable timber production (two mixtures), the protection against wildfire (two mixtures), biodiversity (two mixtures) and cork production (one mixture). Among other lesser objectives are timber and fuelwood production, ecological stability, social function, conversion to high forests, recreation, biodiversity conservation, aesthetic value and some very specific aims like resin and cone or nut production.

Table 6.15 Challenges of management in the Continental BR

Mixture type	Country	Challenges according to the relevance					
		I	II	III	IV	V	VI
Pa-Fs-Aa	Austria	Steep terrain	High game pressure (browsing of *Aa*)	Taming beech regeneration	–	–	–
Ld-Pa-Pc	Austria	Steep terrain	High game pressure on *Ld*	–	–	–	–
Fs-Qp (Qr) *Fs-Aps-Fe-Qr*	Belgium	Lack of management rules for mixtures	Beech outcompete other species	–	–	–	–
Pm-Pa	Belgium	Lack of management rules for mixtures	–	–	–	–	–
Qp-Qc	Bulgaria	Decreased vitality at some places due to many rotations of coppice management	Lack of successful transformation to seed-originated stands due to insufficient care of newly regenerated seedlings	–	–	–	–
Qr–Cb	Croatia	Natural regeneration of *Qr*	Weed control	High game pressure	–	–	–
Qp-Cb	Croatia	High harvest in private forests	Increase of *Fs* at the expense of *Qp*	–	–	–	–
Ps-Qp-Cb-Tc	The Czech Republic	Regeneration of light-demanding species	Natural regeneration in drought periods	High game pressure	Wood processing industry of non-conifers species	Insufficient knowledge of mixed stand management	Silviculture of valuable admixtures
Pa-Fs	The Czech Republic	Spruce stability and health	Ecophysiology of thinning	High game pressure	–	–	–
Fs-Aps (Fe)	Denmark	Inter-tree competition, mixture management	–	–	–	–	–

(continued)

Table 6.15 (continued)

Mixture type	Country	Challenges according to the relevance					
		I	II	III	IV	V	VI
Fe-Ag	Denmark	Ash dieback	–	–	–	–	–
Psy-Fs	Germany	Unknown behaviour of tree species response to climate change	High browsing pressure	Role of pests in a warmer climate	High establishment costs for oak regenerations	–	–
Qr-Cb-Fspp-Um-Aspp	Italy	Hornbeam control to allow growth of oak regeneration	Valorization of sporadic tree species	Relatively high pressure from ungulates	Increase the provision of non-wood forest products	–	–
Oc-Fo-Qpu	Italy	Lack of management in steep slopes	Silvicultural abandonment can produce serious problems of stand stability	Technological innovation for wood valorization	Relatively high pressure from ungulates	Increase the provision of non-wood forest products	–
Psy-Qr (Qp)	Poland	High game pressure	–	–	–	–	–
Fs-Qr (Qp)	Poland	High game pressure	Strong competition caused by *Fs* at naturally regenerated stands	–	–	–	–
Qr-Fa	Serbia	Obtaining natural regeneration	Dead trees or groups of trees	High game pressure	Weed control	Climate change impacts	–
Qc-Qf	Serbia	Coppice origin, conversion	High harvest in private forests	Decreased vitality at some places due to many rotations of coppice management	–	–	–
Ps-Qr	Ukraine	Preservation of *Qr* natural regeneration	Dominance of artificial regeneration	Negative impact of fast-growing species	–	–	–
Qr-Cb	Ukraine	Lack of natural regeneration of *Qr* and dominance of *Cb*	Insufficient care for plants at a young age	Management models for mixtures	–	–	–

Fig. 6.12 Countries in the Mediterranean BR participating in the survey (*BA* Bosnia and Hercegovina, *HR* Croatia, *GR* Greece, *IT* Italy, *PT* Portugal, *ES* Spain, *TR* Turkey)

6.3.6.2 Silvicultural Prescriptions

Apart from Bosnia and Hercegovina where no interventions are foreseen in Mediterranean forests, the main regeneration system used is the shelterwood system with natural regeneration sometimes supplemented by artificial planting or seeding. The clear-cutting is applied in four mixtures (Italy, Portugal and Turkey) (Table 6.17). Coppicing methods are also common in this region (Italy, Greece). In Portugal management of *Quercus suber*-*Pinus pinea* mixed stands is based on the irregular shelterwood system; however, cork oak is protected by law. The regeneration period is commonly 20 years with some exceptions that can reach up to 30 (or 40) years in Italy. Rotation age differs substantially between mixtures being from 30 years (*Quercus* spp.) to 140 years (*Fagus sylvatica*-*Abies alba*) in Italy. The target DBH like rotation age is also diverse ranging from 10–15 cm (Italy) to 50 cm (Greece, Italy, Portugal and Turkey). Both the rotation age and the target DBH strongly depend on tree species and on the regeneration method. Release treatments like weeding, cleaning and brushing are performed in almost all mixtures except Bosnia and Hercegovina and one type in Italy. Among thinning methods, the most common one is thinning from below used in five mixtures. Intermediate, crown and selective thinning are less frequent. Thinning intensity ranges from 10% to 15% (Croatia,

Table 6.16 Management objectives in the Mediterranean BR

Mixture type[a]	Country	Silvicultural objective according to the relevance			
		I	II	III	IV
Qpu-Co[2]	Bosnia and Hercegovina	Protection against wildfire	–	–	–
Qpu-Oc[2]	Bosnia and Hercegovina	Protection against wildfire	–	–	–
Qpu-Co[4]	Croatia	Protection (soil, water)	Social functions	Conversion to high forests	–
Qi-Fon[4]	Croatia	Protection (soil, water)	Social functions	Conversion to high forests	–
Fs-Psy-Pa[4]	Greece	Biodiversity	High productivity	Ecological stability	Aesthetic value
Qi(Qco/Au/Aad)-Ph (Pp/Cse)[4]	Greece	Biodiversity	Ecological stability	–	–
Fs-Aa[4]	Italy	Protection (soil, water)	Biodiversity conservation	Timber production	–
Qspp(*Qi*/*Qp*/*Qce*)-Mediterranean *Pspp* (*Ph*/*Pp*/*Ppr*)[4]	Italy	Protection (soil, water)	Fuelwood production (*Qspp.*)	Recreation (coastal pinewoods)	–
Qs-Pp[4]	Portugal	Cork production (*Qs*)	Cone production (pine nuts) and wood	–	–
Cs-Pm[4]	Portugal	Valuable timber (*Cs*); Timber of small, medium and large dimensions (*Pm*)	*Pm* promotes well-shaped *Cs*	–	–
Psy(*Ppr*)*-Qpy*[1]	Spain	Protection (soil, water)	Timber (*Psy* and *Ppr*), biomass production (*Qpy*)	Resin (*Ppr*)	Biodiversity
Pb-Cl[4]	Turkey	Valuable timber production	Fuelwood	–	–
Cl-Ac-Jspp[4]					

[a] The mixture was defined according to the percentage of tree species in [1] basal area, [2] volume, [3] stem number, [4] and canopy cover

Fig. 6.13 *Quercus suber* L.-*Pinus pinea* L. mixture forest in the Mediterranean BR (Portugal) (Source: S. Barreiro)

Italy) of the growing stock to up to 30–40% in the terms of the number of trees for *Pseudotsuga menziesii* in mixture *Castanea sativa-Pseudotsuga menziesii* (Portugal). The frequency of thinning is mostly one entry per 10 years or depends on commercial profitability or the stage of stand development. In the majority of mixtures, salvage and sanitation cuttings are applied. In Portugal, artificial pruning of the main species in both mixtures and fertilization in *Quercus suber-Pinus pinea* may be used. The potential for tree species diversification is indicated as limited in six mixtures, and no such possibility is considered in two cases and foreseen possible in three mixtures.

6.3.6.3 Challenges of Management

The commonest challenge identified in the region is gaps in the knowledge on the management of mixed stands (Table 6.18). This was the highest-ranked challenge in the case of four mixtures (Greece, Portugal and Spain) and received a lower rank in two other mixtures. High game pressure is the second-ranked challenge in two mixtures (Croatia) as the major issue and as a minor problem in one other case (Italy). Other important challenges are species interactions in the condition of the closed canopy (two mixtures in Bosnia and Hercegovina), a shift from timber-oriented management to other objectives like biodiversity protection (two mixtures in Turkey) and lack of technical, management guidelines (Portugal). The remainder of the challenges reported had lower rankings.

Table 6.17 Silvicultural prescriptions in the Mediterranean BR

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Qpu-Co	Bosnia and Hercegovina	NA	NA	NA	NA	NA	NA	NA	NA	ND
Qpu-Oc	Bosnia and Hercegovina	NA	NA	NA	NA	NA	NA	NA	NA	ND
Qpu-Co	Croatia	SH	NR (AP, AS)/10–20	80/40	Y (W,B, C)	CT	10–15	1 per 10 years	SLC, SNC	L
Qi-Fo	Croatia	SH	NR (AP, AS)/10–20	80/40	Y (W,B, C)	CT	10–15	1 per 10 years	SLC, SNC	L
Fs-Psy-Pa	Greece	SH, CO	VR/10–20	80/50	Y (C)	SVT	15–20	1 per 10 years	NA	L
Qi(Qc/Au/Aa)-Ph(Pp/Cse)	Greece	CO	VR/10–20	80/50	N	SVT	15–20	1 per 10 years	NA	L
Fs-Aa	Italy	SH, IS, (SS, GS)	NR/20–40	90–140/ 40–50	Y (in public property)	LT or SVT	15–25	Depends on commercial profitability	NA	Y
Qspp(*Qi*/*Qp*/ *Qc*)-Mediterranean *Pspp*(*Ph*/ *Pp*/*Ppr*)	Italy	CC, SH, CS	NR, AP/10–30	30 (*Qspp*), 80–100 (*Pspp*)/ 10–15	N	LT in pine	10–15	Depends on commercial profitability	NA	L

Qs-Pp	Portugal	IH	AP/NA	120 (*Pp*)/NA	Y (W,C)	LT, SVT	20–30 (*Qs-Pp*) (trees removed)	1 per 10 years/4–5 (*Qs*); 1 per 5–10 years/ 2–4 (*Pp*)	PR (*Qs*,*Pp*), FE (*Qs-Pp*), SNC (*Pp*)	N
Cs-Pm	Portugal	CC	AP/NA	40–45 (*Cs*,*Pm*)/ 40–45 (*Cs*) 40–50 (*Pm*)	N	IT	30–40 (*Pm*); 20–40 (*Cs*) (trees removed)	1 per 7–10 years/3 (*Pm*); 1 per 7 years/4 (*Cs*)	PR (*Cs*,*Pm*), SLC, SNC	N
Psy/Ppr-Qpy	Spain	SH	NR/≥20	100–120	Y (if needed)	LT	20–35	Depending on stage of development	SLC, SNC	L
Pb-Cl	Turkey	CC	NR (Pb), AS (*Cl*)/NA	60/45 (*Pb*), 120/50 (*Cl*)	Y	LT	20–25	2	SLC, SNC if needed	Y
Cl-Ac-Jspp	Turkey	CC	NR/NA	120/50	Y	IT	20–25	2	SLC, SNC if needed	Y

Table 6.18 Challenges of management in the Mediterranean BR

Mixture type	Country	Challenges according to the relevance			
		I	II	III	IV
Qpu-Co	Bosnia and Hercegovina	Species interaction in condition of closed canopy	–	–	–
Qpu-Oc	Bosnia and Hercegovina	Species interaction in condition of closed canopy	–	–	–
Qpu-Co	Croatia	High game pressure	Tourism	Climate change impacts	
Qi-Fo	Croatia	High game pressure	Tourism	Climate change impacts	
Fs-Psy-Pa	Greece	Gaps in management knowledge	–	–	–
Qi(Qc/Au/Aa)-Ph(Pp/Cse)	Greece	Gaps in management knowledge	–	–	–
Fs-Aa	Italy	Management limited due to mixture occurrence in protected areas	Silviculture of pure beech/fir stands towards multispecies forests with distinctive valorization of sporadic tree species	Relatively high pressure from ungulates	–
Qspp(*Qi*/*Qp*/*Qc*)-Mediterranean *Pspp*(*Ph*/*Pp*/*Ppr*)	Italy	Small size properties, lack of specific management rules	Fire prevention and fostering more fire-resilient stands	Valorization of sporadic tree species	Increase the provision of non-wood forest products
Qs-Pp	Portugal	Lack of knowledge about how both species grow in the mixture	Lack of technical, management guidelines	–	–
Cs-Pm	Portugal	Small size properties	Lack of technical, management guidelines	Reduction of interest in the demand for chestnut wood	Low interest of owners in forest management

(continued)

Table 6.18 (continued)

Mixture type	Country	Challenges according to the relevance			
		I	II	III	IV
Psy(Ppr)-Qpy	Spain	Knowledge how to grow mixtures	Fire occurrence	Climate change impacts	–
Pb-Cl	Turkey	Management focuses on other objectives (e.g. diversity)	Lack of information on the growing different mixtures	–	–
Cl-Ac-Jspp	Turkey	Management focuses on other objectives (e.g. diversity)	Lack of information on the growing different mixtures	–	–

6.3.7 Anatolian, Pannonian and Steppic Biogeographical Region

6.3.7.1 Mixture Types and Management Objectives

The Anatolian, Pannonian and Steppic biogeographical regions are represented only by three countries that replied to the survey (Fig. 6.14). The dominant tree species in these regions are *Quercus* spp., *Pinus nigra*, *Pinus sylvestris* and *Juniperus* spp. (Table 6.19). The share of species in the mixtures is determined based on a percentage of canopy cover and volume. The most important management objective in the region is valuable timber production (first ranked in three mixtures in Slovakia and Ukraine; lower ranking in two mixtures in Turkey). The next is the protection of soils and water which was indicated in two mixtures in Turkey as the highest priority and of lower importance in three mixtures in Slovakia and Ukraine.

6.3.7.2 Silvicultural Prescriptions

The clear-cutting is the dominant regeneration system in the regions (Table 6.20). In Slovakia, the shelterwood system is applied in *Quercus petraea-Carpinus betulus* mixtures followed by natural regeneration with the regeneration period lasting 30–40 years. In Turkey, the coppice system is used for *Quercus* spp.-*Juniperus* spp.-*Prunus* spp. mixture with vegetative renewal. In the clear-cutting methods, regeneration relies on artificial planting or seeding. Rotation age differs significantly depending on the tree species. It ranges from 30 years for the coppice and clear-cutting systems in Turkey (Anatolian and Steppic) to 150 years in Slovakia (Pannonian) for the shelterwood method. Likewise, the target DBH varies from

Fig. 6.14 Countries in the Anatolian, Pannonian and Steppic BRs participating in the survey (*SK* Slovakia, *TR* Turkey, *UA* Ukraine)

Table 6.19 Management objectives in the Anatolian, Pannonian and Steppic BRs

Mixture type[a]	Country[b]	Silvicultural objective according to the relevance	
		I	II
Pn-Jspp-Qspp[4]	Turkey (A)	Protection (soil, water)	Timber production
Qspp-Jspp-Prspp[4]			
Qp-Cb[2]	Slovakia (P)	Valuable oak timber production	Protection (soil, water)
Pn-Jspp-Ad[4]	Turkey (S)	Protection (soil, water)	Valuable timber production
Jspp-Qspp-Ad-Prspp-Crspp[4]			
Qr-Ap-Tc[2]	Ukraine (S)	Valuable timber production	Protection (soil)
Psy-Qr[2]	Ukraine (S)	Valuable oak and pine timber	Protection (soil)

[a] The mixture was defined according to the percentage of tree species in [1] basal area, [2] volume, [3] stem number and [4] canopy cover

[b] *A* Anatolian, *P* Pannonian, *S* Steppic

Table 6.20 Silvicultural prescriptions in Anatolian, Pannonian and Steppic BRs

Mixture type	Country[a]	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/ target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Pn-Jspp-Qspp	Turkey (A)	CC	AP/NA	120/50	Y (L,W)	IT	20	1	SLC, SNC if needed	Y
Qspp-Jspp-Prspp	Turkey (A)	CO	VR/NA	30/20	Y (L)	CRT	20	1	SLC, SNC if needed	Y
Qp-Cb	Slovakia (P)	SH	NR/30–40	130–150/ 55–60	Y (W)	CT, CRT	14–18	5–7(10)/ 5–7	SLC, SNC	L
Pn-Jspp-Ad	Turkey (S)	CC	NR, AS/NA	30/20	Y (L)	CRT	20	1	SLC, SNC if needed	Y
Jspp-Qspp-Ad-Pspp-Cspp	Turkey (S)	CC	AP/NA	30/20	Y (L)	CRT	20	1	SLC, SNC if needed	Y
Qr-Ap-Tc	Ukraine (S)	CC	AP, AS/10	100–110/ 25–30	Y (W)	CT, IT, LT (depending on age)	5–7–10–20	5–7–10–15–25/ 1–2	SLC (if needed), SNC, FE	Y
Psy-Qr	Ukraine (S)	CC	AP/10	80–90/ 30–35	Y (W)	LT	7–10-15	5–7–10–15–20/ 1–2	PR, SLC, FE	Y

[a] *A* Anatolian, *P* Pannonian, *S* Steppic

20 cm (Turkey) to 60 cm (Slovakia). Release treatments (weeding, liberation) are performed in all listed mixtures. The most widespread methods of thinning are final crop thinning and crown thinning (from above). Thinning from below, intermediate thinning or thinning method depending on age are indicated in some countries. The intensity of thinning does not exceed 15–20% of the growing stock. The frequency of thinning depends on the stage of stand development and ranges from 5 to 20 (or 25) years. In Turkey thinning is performed only once in the rotation. In all mixtures, salvage and sanitation cuttings are applied. Additionally, in Ukraine, some fertilization and artificial pruning are allowed. The potential for tree species diversification is reported in almost all mixtures except for *Quercus petraea-Carpinus betulus* type in Slovakia which is pointed as limited.

6.3.7.3 Challenges of Management

The transformation from timber-oriented management to management focused on other objectives like protection of biodiversity is the main challenge in Turkey (Table 6.21). Other important challenges involve the protection and maintenance of natural regeneration of mixed stands, especially of *Quercus robur* and *Quercus petraea*. Less significant challenges include damage to vegetation by fire, the dominance of artificial over natural restoration, the negative impact of fast-growing species, the improvement of care for plants after planting, the need for improved felling practices in order to ensure natural regeneration of species and foresters' inadequate knowledge about the management of mixed stands.

6.3.8 Mediterranean and Temperate Forest Ecosystems Outside Europe

6.3.8.1 Mixture Types and Management Objectives

Only four countries from outside Europe have responded to our questionnaire (Fig. 6.15). More accurate characteristics of mixed-species forests in South America are presented in Chap. 8 of this book (Loguercio et al. 2018). Species composition of the listed mixed forests in these countries strongly depends on the region (climatic conditions) (Table 6.22, Figs. 6.16 and 6.17). The two main objectives of the management in these forests are the protection of soil and water (Algeria) and valuable timber production (Chile, Morocco). Also, valuable cork production, conservation of *Austrocedrus chilensis* because of *Phytophthora austrocedri* disease and multipurpose management are highly ranked objectives. The remaining aims are very varied and cover, among others, social function, aesthetic value and recreation, ecosystem protection, biodiversity, ecological stability, timber and cork production and restoration of degraded forests.

Table 6.21 Challenges of management in Anatolian, Pannonian and Steppic BRs

Mixture type	Country[a]	Challenges according to the relevance				
		I	II	III	IV	V
Pn-Jspp-Qspp	Turkey (A)	Management focuses on other objectives (e.g. diversity)	–	–	–	–
Qspp-Jspp-Pspp	Turkey (A)	Management focuses on other objectives (e.g. diversity)	–	–	–	–
Qp-Cb	Slovakia (P)	Problems with natural regeneration of *Qp* (wild boar)	The loss of *Qp* seedlings/saplings due to strong competition of *Cb*	–	–	–
Pn-Jspp-Ad	Turkey (S)	Management focuses on other objectives (e.g. diversity)	–	–	–	–
Jspp-Qspp-Ad-Pspp-Cspp	Turkey (S)	Management focuses on other objectives (e.g. diversity)	–	–	–	–
Qr-Ap-Tc	Ukraine (S)	Complexity of natural conditions for natural regeneration of mixed stands	Damages to vegetation because of fires	The loss of a significant part of the trees of *Qr* at the age up to 10 years	Improvement of care for plants	Inadequate knowledge of the foresters on mixed stands management
Psy-Qr	Ukraine (S)	Problems with the preservation of *Qr* natural regeneration	Dominance of artificial over natural restoration	Negative impact of fast-growing species	Improvement of major felling practice in order to ensure a natural regeneration of species	–

[a] *A* Anatolian, *P* Pannonian, *S* Steppic

Fig. 6.15 Non-European countries participating in the survey (*DZ* Algeria, *AR* Argentina, *CL* Chile, *MA* Morocco)

6.3.8.2 Silvicultural Prescriptions

The most common regeneration methods are the uniform and irregular shelterwood systems (Table 6.23). For *Quercus rotundifolia* in Morocco, the coppice system is also applied. Natural regeneration or artificial planting is the commonest in the listed mixtures. The regeneration period is mostly between 15 and 25 years, but in Algeria, it is longer up to 40 years. The rotation age ranges from 40 years for *Quercus rotundifolia* managed by coppicing in Morocco to 70 years in *Nothofagus obliqua-Nothofagus alpina* mixture leaving old-growth remnants (125 years) to be incorporated into the following generation where it seems to be economically promising by irregular shelterwood in Chile. The target DBH is described in four mixtures and is from 45 cm for *Nothofagus dombeyi* in *Austrocedrus chilensis-Nothofagus dombeyi* type (Argentina) and *Nothofagus obliqua-Nothofagus alpina* type (Chile) to 80 cm in Morocco. In all mixture types, some release treatments (weeding, brushing, cleaning) are performed. The main thinning methods are crown and intermediate thinning, but also free thinning and thinning similar to salvage cuttings are used. The intensity of thinning in most mixtures depends on stand age and stand density, and precise details are not available. Similarly, the frequency of thinning depends on stand age and density in Argentina or is from 10 (Chile) to 20 (Morocco) years. Among other intermediate treatments, the most common intervention is artificial pruning which is performed in Morocco and could be possible in Argentina. Salvage and sanitation cuttings are used only in Algeria and in *Austrocedrus chilensis-Nothofagus dombeyi* types in Argentina. In mixtures indicated in Algeria, no thinning is applied. The potential for tree species diversification was marked for mixtures in Algeria and Chile. In other mixed types, this aspect is not reported or there are no such possibilities.

Table 6.22 Management objectives in some specific mixtures in the Mediterranean and temperate forest ecosystems outside Europe

Mixture type	Country	Silvicultural objective according to the relevance				
		I	II	III	IV	V
Qs-Ph-Qi-Qfa	Algeria	Protection (soil, water)	Restoration of forest *Qs* because not natural regeneration	Valuable cork production	Social functions	Aesthetic value and recreation
Ca-Qs-Qi-Ph	Algeria	Protection (soil, water)	Restoration of degraded forest of degraded *Ca* because not natural regeneration	Biodiversity conservation	Social functions	Aesthetic value and recreation
Ach-Nd	Argentina	Conservation of *Ach* because of *Phytophthora austrocedri* disease	Restoration of degraded *Ac* forests	Timber production of *Ac* and *Nd*	–	–
Na-No-Nd	Argentina	Multipurpose management	Valuable timber production	Ecosystem protection (soil, water, biodiversity)	Aesthetic value preservation	Scientific research
No-Na with temperate rainforest species	Chile	Valuable timber production	Biodiversity	Ecological stability	–	–
Ca-Qrt	Morocco	Valuable cedar timber and oak timber as fuelwood	–	–	–	–
Qrt-Qs	Morocco	Valuable cork	Valuable oak timber	–	–	–

Fig. 6.16 *Nothofagus dombeyi* (Mirb.) Oerst.-*Austrocedrus chilensis* (D.Don) Pic.Serm. & Bizzarri mixture forest in the sub-Antarctic temperate region of Argentina. (Source: G. Loguercio)

Fig. 6.17 *Cedrus atlantica* (Endl.) Manetti ex Carrière-*Quercus rotundifolia* Lam. mixture in the Medal Atlas forest, humid bioclimate, Morocco. (Source: B. Belghazi)

Table 6.23 Silvicultural prescriptions in some specific mixtures in the Mediterranean and temperate forest ecosystems outside Europe

Mixture type	Country	Silvicultural system	Type of regeneration/ regeneration period [years]	Rotation [years]/target DBH [cm]	Release treatments	Thinning			Other intermediate treatments	Potential for tree species diversification
						Method	Intensity of growing stock removal [%]	Frequency [years]/ number of entries		
Qs-Ph-Qi-Qfa	Algeria	IS	AP, NR/≥40	NA	Y (C)	NA	NA	NA	SNC	Y
Ca-Qs-Qi-Ph	Algeria	IS	AP, NR/≥40	NA	Y (C)	NA	NA	NA	SNC	Y
Ach-Nd	Argentina	Combination GS for *Nd* and SLC for *Ach*	NR/–	Regulated by SLC (*Ach*)/ 45(*Nd*)	Y (C)	CRT (*Nd*) SLC (*Ach*)	Depending on stand age and density	Depending on stand age and density	PR(*Nd*) if needed, SLC	ND
Na-No-Nd	Argentina	SH	NR/20	100/–	Y	CT	Depending on stand age and density	Depending on stand age and density	NA	N
No-Na with temperate rainforest species	Chile	IS	NR, VR/≥15	70 (125 for old-growth incorporated into next generation)/ 45–50	Y (C)	CT, FT	Depending on natural density (maintaining 35% of rel. density)	10/3 (*No-Na*); 10/3 (others)	NA	Y
Ca-Qrt	Morocco	SH(*Ca*), CO (*Qrt*)	NR, AP(Ca)/ ≥20	120(*Ca*), 40 (*Qrt*)/80(*Ca*)	Y (W,B, C)	IT	Depending on stand age and density	40 then each 20 (*Ca*)	PR(*Ca*)	ND
Qrt-Qs	Morocco	SH(*Qs*), CO (*Qrt*)	NR, AP(Qs)/ 20–24	120(*Qs*), 40 (*Qrt*)/80(*Qs*)	Y (W,B, C)	IT	Depending on stand age and density	Each 20 (*Qs*)	PR(*Qs*)	ND

6.3.8.3 Challenges of Management

The most significant challenge for these mixtures is to control overgrazing which is mentioned in all mixtures (Algeria, Argentina, Chile and Morocco) (Table 6.24). Two others given the highest rank are conservation of *Austrocedrus chilensis* against *Phytophthora* through natural regeneration (Argentina) and the problem with regeneration due to bamboo competition (Chile). From the remaining challenges, illegal cutting practice (Algeria, Morocco), problems with the preservation of *Quercus suber* natural regeneration (Algeria), lack of application of management plans (Morocco), lack of knowledge on how yield and growth of the main tree species might be affected by climate change (Morocco) and damages to vegetation by fire (Algeria) are often reported.

6.4 Discussion and Conclusion

Although not all countries replied to the questionnaire, the response level reached 58% which is a high level for this type of survey (Baruch and Holtom 2008). Furthermore, the response allows us for the first time to assess the state of silviculture in mixed stands across most of Europe including all nine biogeographical regions, as well as allowing comparison with a few countries outside the continent. However, we are aware that this study may have some limitations like some bias in the mixture selection (as it should be well-described), possible bias due to the fact that in many cases the information was provided by researchers and difficulties to cover all the possible particularities in silvicultural treatments.

Forests in Europe cover a large bioclimatological range from the Boreal to the Mediterranean regions and from floodplain to mountain areas up to the alpine tree line (FOREST EUROPE 2015). As a consequence, species composition and the type of mixtures in European forests are very varied. Mixed forests dominated by conifers are prevalent in the Alpine (*Abies alba*, *Picea abies*), Atlantic (*Pinus sylvestris*, *Picea abies*, *Picea sitchensis*) and Boreal (*Picea abies*, *Pinus sylvestris*) regions, while broadleaves are prevalent in the Black Sea, Continental, Mediterranean, Pannonian and Steppic regions. The mixed stands in the Alpine region are mainly composed of *Abies alba*, *Picea abies* and *Fagus sylvatica* in different configurations and proportions so that the management of these mixtures is similar in many cases. Similarly, mixtures in the Boreal BR consist mostly of three tree species: *Picea abies*, *Pinus sylvestris* and *Betula pendula*. By contrast, species diversity in the remaining BRs is much higher so that it is rather difficult to indicate dominant species. The mixtures can be defined according to various stand parameters like basal area, volume, stem number, canopy cover and biomass (Dirnberger et al. 2017; del Río et al. 2018), but the most common definitions used in all BRs are volume and canopy cover. That is the reason for some difficulties in comparing different types of mixed stands within and between BRs.

Table 6.24 Challenges of management in some specific mixtures in the Mediterranean and temperate forest ecosystems outside Europe

Mixture type	Country	Challenges according to the relevance			
		I	II	III	IV
Qs-Ph-Qi-Qfa	Algeria	Overgrazing	Problems with the preservation of *Qs* natural regeneration	Illegal cutting practice	Damages to vegetation because of fires
Ca-Qs-Qi-Ph	Algeria	Overgrazing	Problems with the preservation of *Ca* natural regeneration	Illegal cutting practice	Damages to vegetation because of fires
Ach-Nd	Argentina	Conservation of *Ach* against *Phytophthora* through natural regeneration, overgrazing by domestic cattle	Growth relationships in mixed stand to regulate composition	Production of quality timber (*Nd*)	–
Na-No-Nd	Argentina	Overgrazing by domestic cattle	Large crown cover of remnant trees after harvesting	Dense understory of *Chusquea culeou*	–
No-Na with temperate rainforest species	Chile	Overgrazing, problem with regeneration due to bamboo occurrence	Little experience in satisfactory regeneration of valuable tree species	More information about strip width and gap size is needed	–
Ca-Qrt	Morocco	Overgrazing	Lack of application of the management plan	Illegal cutting practice	Lack of knowledge on yield and growth of the main tree species considering climate change
Qrt-Qs	Morocco	Overgrazing	Lack of application of the management plan	Illegal cutting practice	Lack of knowledge on yield and growth of the main tree species considering climate change

Despite the increasing attention paid to the ecological role of forests, when considering the highest-ranked management objectives, timber production, and in particular valuable timber production, represents the major driver of mixed forest management in Europe and in selected mixtures outside Europe (Fig. 6.18). Protection of soil and water as well as protection of forests against disturbances (e.g. fire,

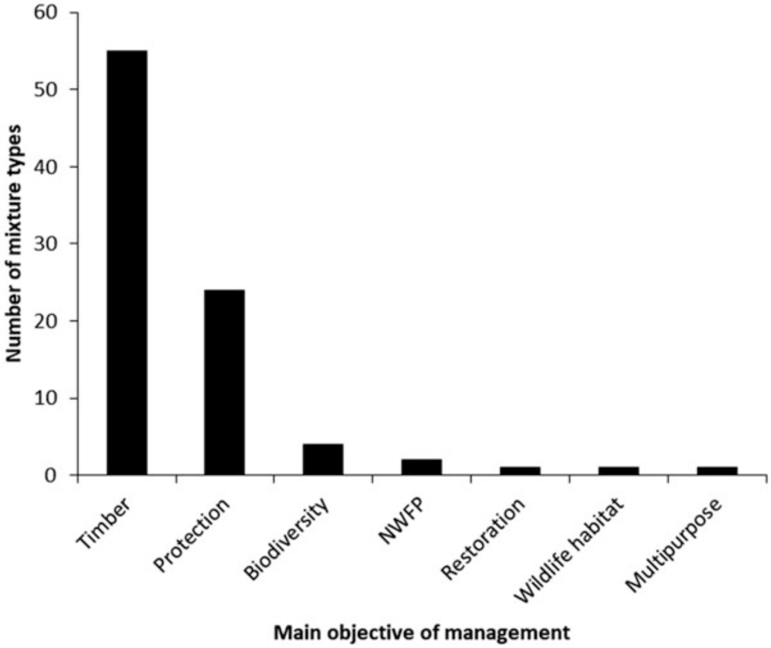

Fig. 6.18 The main management objectives in the studied mixture types (*NWFP* non-wood forest products (nuts, cork))

diseases, avalanches, rockfalls and landslides) is the second most important management goal followed by other aims like biodiversity, non-wood forest products (nuts, cork), restoration of native woodlands, wildlife habitat and multipurpose management (Biber et al. 2015). The outdoor recreation activities and nature-based tourism, which are not clearly mentioned by respondents in the survey, have rapidly expanded from protected areas into commercial forests (Tyrväinen et al. 2014), and in many European countries, they are recognized as the most valuable forest ecosystem service provided. Setting up aesthetic value of forests, Ribe (1989) highlights such their attributes as openness and visibility, amount of light in the stand and its stratification, but at the same time, he also suggests that there is a slight overall preference for species diversity. In fact, most often mixed forests are preferred by visitors over monocultures which is grounded on the recreational value of this forest type (Gundersen and Frivold, 2008; Schraml and Volz 2009; Edwards et al. 2012; Carnol et al. 2014; Giergiczny et al. 2015). Thus forest managers should recognize these new challenges and deal with them proactively rather than reactively (Tyrväinen et al. 2014, 2017). Consequently, this should lead sometimes to modification of the applied forest management regimes.

Still, in Europe, much attention is evidently paid to valuable timber production as the means of covering the costs of all other treatments in forests while providing a certain level of profit to the landowner. Since timber quality coming from mixed

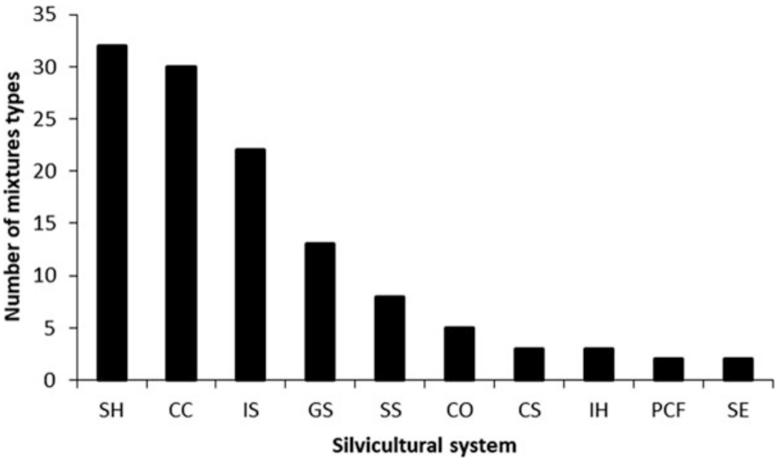

Fig. 6.19 The silvicultural systems applied in the studied mixture types (*CC* clear-cutting, *CO* coppice, *CS* coppice-with-standard system, *GS* group selection, *IH* individual tree harvesting, *IS* irregular shelterwood, *PCF* patch clear felling, *SE* selection, *SH* shelterwood, *SS* single tree selection)

stands is generally lower than from pure stands (Röhrig et al. 2006), much more effort is required to obtain valuable timber from a multispecies stand. If uncertainty and reduced financial risk (production risk) are taken into consideration, mixed stands can show advantages in comparison to the pure stands (Griess and Knoke 2013; Knoke 2017).

The silvicultural systems mentioned by respondents in the questionnaires were varied covering almost all techniques used in the temperate region (Matthews 1991). Just as site conditions, ownership, cultural, economic and social conditions vary, so forest management should differ and be adjusted to local conditions (Spiecker 2003). The uniform shelterwood is the most widespread regeneration system (Fig. 6.19) applied mostly in Continental, Alpine and Mediterranean BRs followed by the clear-cutting system (Boreal, Atlantic BRs) and the irregular shelterwood system (Alpine, Continental BRs). The use of specific regeneration methods entails the application of natural or artificial regeneration. Both the uniform and irregular shelterwood systems are based on the use of natural regeneration, while the clear-cutting system depends upon planting (artificial regeneration). Some complementary artificial planting may be used to enrich natural regeneration and vice versa: this can be a means of creating some valuable admixtures. Other local regeneration methods are carried out according to the type of mixture and the main silvicultural objectives. We found in our study that single tree or group selection systems that are mostly used in forests composed of shade-tolerant species are usually combined with valuable timber production. Among less representative but locally important regeneration methods is coppicing in the Mediterranean, Atlantic and Anatolian BRs (less frequent in Continental BR and Morocco too) where it has a long and well-established tradition.

From the point of view of the potential of species diversification in listed mixtures, temporal and spatial separation of species regeneration within a stand is a very powerful way to increase species heterogeneity of forest stands (Bauhus et al. 2017). This is a fundamental assumptions of the irregular shelterwood system that fosters the regeneration of tree species with various functional traits (Bagnaresi et al. 2002; Raymond et al. 2009; Klopcic and Boncina 2012; Pretzsch et al. 2015a; Raymond and Bédard 2017) at the same time taking care of the value increment (growth potential, high-quality timber) of mature trees (Paluch 2006; Skrzyszewski et al. 2017). Even in Scandinavian conditions (Boreal BR) where clear-cutting is a dominant regeneration method, some possibilities exist to enhance species diversification (Holmström et al. 2016).

The Boreal BR should be considered an outlier in this survey as, in the countries belonging to this region, an intensive silviculture, focused on timber production, is still the dominant approach. In this case, the main regeneration method employed is clear-cutting followed by artificial regeneration, although some differences are evident in the case of broadleaved natural regeneration (mostly *Betula* spp.). In this BR intensive interventions such as fertilization, mechanical soil preparation and weeding are common. A further example of intensive silviculture, however, is shown in a contrasting climatic condition, in a few mixtures of the Mediterranean BR. Here forest types like cork oak- and chestnut-dominated forests are under a strict management (including fertilizing practices) to guarantee productive purposes. In general such practices as fertilization, soil liming and chemical control are associated with a high interest in productivity goals.

The most frequent thinning method in all studied regions is crown thinning (from above), especially in Continental and Alpine BRs (Fig. 6.20). This method concentrates on the selection of the best crop trees in the main canopy of the stand and elimination of one or two most competitive trees from the same strata. Low thinning

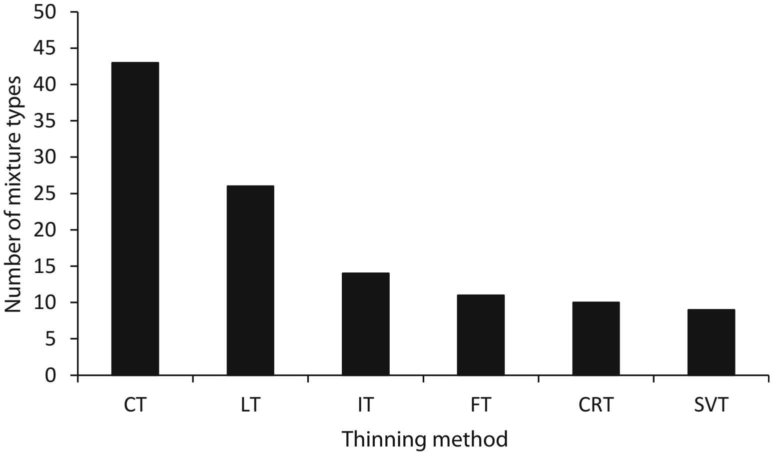

Fig. 6.20 Number of mixture types according to indicated thinning methods in all BRs (*CRT* final crop thinning, *CT* crown thinning, *FT* free style of thinning, *IT* intermediate thinning, *LT* low thinning, *SVT* selective thinning)

(from below) which is the second most common method, especially in Boreal BR where it is used in 75% of the mixtures, operates in the lower stand strata removing suppressed and intermediate trees without paying attention to the trees in the upper layer. The frequency of occurrence of other methods (free, intermediate, crop tree and selective thinning) is similar. Differences in growth pattern and rates, tree allometry, species interactions and crown shape between mono- and multispecies stands are evident (Pretzsch and Forrester 2017; Pretzsch 2017), and application of thinning methods developed in monospecific stands in mixed-species forests can be inaccurate and even flawed (Bauhus et al. 2017). An alternative solution for mixed stands could be the use of the thinning method, called crop tree thinning, indicated in a few mixtures, focusing on individual trees in the stand considering the species proportion, spatial and temporal mixing pattern, relative growth rates of neighbouring trees and species-specific target diameters (Bauhus et al. 2017).

The replies to the questions on challenges let us identify how important was an effective sustainable management of the mixtures. Indeed, management aspects are the most important of the challenges listed. The second aspect, in order of importance, is the problem of regeneration, first, if we consider that many described mixtures are managed by adopting artificial regeneration, at the place of or integrating the natural one. Considering the third aspect of improving knowledge about the dynamics and growth of mixtures, we can say that studies are needed to better understand the functioning of each one of the mixtures described. With such additional knowledge, it will be possible to develop more site-specific management guidelines. Regional topics included the serious impact of environmental (biotic and abiotic) factors on forest stability and functionality as in the Mediterranean area, in consequence of wildfires and climate change, or over a wider region for the game pressure.

Considering only those challenges given the highest ranking, the main issue is high browsing pressure from game animals (also including domestic animals), which threatens target species composition of regeneration (Klopcic et al. 2010; Bernard et al. 2017). Regeneration is threatened by animals during both seedling (browsing, trampling, fraying) and sapling stages (bark stripping). A lot of measures and efforts need to be made in order to ensure the survival of appropriate species composition of regeneration (Hothorn and Müller 2010; Beguin et al. 2016). The second most important challenge is the lack of management rules covering mixture growth and taking into account both species functional traits and site conditions. There is an urgent need to fill this gap in our knowledge of mixed forest management (Pretzsch and Zenner 2017; Coll et al. 2018), especially in the face of predicted environmental changes (IPCC 2014). Problems to get natural regeneration of specific tree species (*Picea abies*, *Pinus sylvestris*, *Quercus petraea*, *Quercus robur*) in the some site and stand conditions (hornbeam or bamboo occurrence) are the third of the highest-ranked challenge. A significant challenge, surprisingly listed in only a few cases, is climate change impacts on growth and performance of tree species, although the establishment of mixtures is seen as a promising tool to adapt forest ecosystems to climate change (Ammer 2017).

Responses to the survey indicated that potential for tree species diversification exists in analysed mixtures (43 mixed types) however depending on climatic conditions. The largest potential is in Continental, Black Sea, Anatolian, Steppic and Atlantic BRs. In 26 listed mixtures, the potential was determined as limited (ten in Alpine BR) due to unfavourable site conditions, and in six ones (Alpine, Mediterranean, one in Argentina), such possibilities do not exist. The secondary temperate forests of Chile have a great potential for diversification with the incorporation of semi-tolerant and tolerant rainforest species. This potential for tree species diversification is very important in the light of enhancing forests' adaptability to predicted environmental (climatic) changes (Bolte et al. 2009; Seppälä et al. 2009; Lindner et al. 2010; Park et al. 2014; Vilà-Cabrera et al. 2018).

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Chapter 7
The Development of Silvicultural Guidelines for Creating Mixed Forests

W. L. Mason, M. Löf, M. Pach, and P. Spathelf

Abstract Recent decades have seen an increase in research interest in mixed forests and greater policy support for measures designed to develop mixed-species stands. However, reports from a range of European countries show many practical difficulties which are hampering the successful implementation of mixed forest management. This is reflected in a widespread lack of guidance to help managers tackle the complicated silviculture of mixed forests. We present case studies from four different countries in Europe which illustrate different aspects of the management of mixed forests. These showed that successful introduction of a range of species depended upon a favourable light climate for the young seedlings and adequate control of browsing animals. The establishment of a mixed stand might take several decades and could require careful tending during the early years. Forest development types (FDTs) have been used in a few countries as a means of defining future stand development goals, and this concept provides a structured mechanism for developing silvicultural guidance for mixed stands. FDTs can be linked to information about the impacts of projected climate change to provide a framework for implementing a site-specific and adaptive silviculture that promotes mixed forests to deliver a range of benefits over time.

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7.1 Introduction

In recent decades there has been a substantial increase in the research effort investigating the functioning and dynamics of mixed-species forests. Evidence for this increase includes a number of books synthesizing available knowledge on this subject (e.g. Cannell et al. 1992; Kelty et al. 1992; Pretzsch et al. 2017) as well as recent overviews seeking to explain the processes influencing the dynamics of mixed forest systems (e.g. van der Plas et al. 2016; Forrester and Bauhus 2016). These research outputs reflect greater policy support for mixed forests in different parts of Europe (e.g. Austria (Sterba 2016), Italy (Barbati and Ferrari 2016), Poland (Pach et al. 2016), Sweden (Löf 2016), parts of the UK (Mason 2016). However, as a result of past afforestation history, a number of European countries still have a relatively high incidence (>40% of the forest area) of single-species forests (e.g. Austria, Belgium, Finland, Iceland, Ireland, Portugal and the UK: Forest Europe 2011). Furthermore, examination of recent country reports about the status of mixed forests in different European countries (Mason et al. 2016) revealed that nearly half had problems that constrained implementation of mixed forest management. These included little tradition of managing mixed stands (Portugal), most forests being managed as monocultures and favouring the most productive species (Sweden), mixtures being disadvantaged by even-aged management (Finland), fragmented knowledge about efficient management of mixtures (France) and a tendency to delay tending measures resulting in suppression of admixed species (Austria). Those countries which reported few problems in implementing mixed forest management tended to have a long tradition of mixed forest management, often implemented through ‘close-to-nature’ forestry (Croatia, Germany, Slovakia: Spathelf 1997; Mason et al. 2016). However, even in such countries, there can be problems converting single-species conifer stands to mixed forests because of constraints such as deer browsing and a lack of seed trees of alternative species (Kucbel et al. 2016).

Thus, although there is widespread support for creating more mixed-species forests and this aspiration is promoted by national policies, successful delivery of these aims appears more problematic. In part this arises from a silvicultural paradigm prevailing in much of Europe which is based on even-aged management and single-species forests. This has resulted in a widespread forestry culture where adoption of alternative silvicultural practices, such as creation of mixed forests, can be hampered by a series of obstacles including a lack of silvicultural expertise (Puettmann et al. 2015). This is supported by a recent survey of the knowledge gaps about management of mixed forests identified by European practitioners (Coll et al. 2018). Amongst the highest ranked problems in this survey was the need to identify silvicultural treatments that would ensure the persistence of the components of a desired mixture over time. When examining the published research that could provide operational guidance on this issue, Coll et al. (op. cit.) found that only limited information was available. They also observed that the lack of evidence on operational aspects extended to other practical management concerns such as the costs (and benefits) involved in the management of mixed stands, as well as the extent to which mixtures may provide greater operational flexibility. The importance of better information about the stability of mixtures over time was also highlighted by Bauhus et al. (2017) who noted the need to consider the compatibility of the component species of a mixture to develop combinations that would require limited silvicultural input. Compatibility in mixture will be influenced by species traits such as comparative growth rate and shade tolerance, as well as by site factors and climate.

The normal way of translating these general principles of mixture dynamics into information that can be used by foresters in the field is through the preparation of operational guidelines that are specific to particular countries or regions and to individual forest types. Such guidelines can cover aspects such as the desired species composition, the pattern of mixture, the preferred regeneration method and the type and intensity of thinning. However, examination of country reports (Mason et al. 2016) revealed that only three countries (Germany, Poland, Slovakia) had guidelines that specifically covered the management of mixtures. These guidelines were often defined for a particular region or state (e.g. Germany) and appeared to be closely linked to the identification of forest development types (FDTs) composed of particular species combinations. This approach had also been followed in Denmark as part of the introduction of nature-based forest management (Larsen and Nielsen 2007). Other countries either had very general guidelines that gave no exact recommendations on species composition in mixture (e.g. Finland), appeared to have guidance that concentrated on individual species rather than on mixtures (e.g. Austria, the UK) or appeared to have no operational prescriptions for mixtures (e.g. Norway, Portugal). This lack of guidance was also noted by Pretzsch and Zenner (2017) who considered that silvicultural guidelines for mixed-species stands, if available, were ‘predominantly vague and qualitative’.

The apparent scarcity of practical guidelines on silviculture of mixtures in different parts of Europe may also reflect a lack of documented long-term research or operational trials relevant to the silviculture of mixed forests. Such trials can be used to explain and demonstrate successful approaches in different forest types (Coll et al. 2018). Furthermore, evidence from such trials could act as case studies to provide information on actual costs associated with mixed forest silviculture as well as the extent of any improvement in management flexibility provided by mixed forests. Therefore, in this chapter, we describe a few long-term examples in different parts of Europe where managers and/or researchers have sought to promote the management of mixtures. We use this information to outline some general principles that can be used by others wishing to develop silvicultural guidance for managers aiming to create successful mixtures that are both sustainable over time and cost-effective to manage.

7.2 Case Studies

7.2.1 Germany

In the eighteenth and nineteenth centuries, there was extensive planting of Scots pine (*Pinus sylvestris* L.) on nutrient poor soils in the north German lowlands (Spathelf and Ammer 2015). Although these forests proved vulnerable to insect pests and fire, for much of the last century, societal demands for increased timber production resulted in the widespread use of silvicultural systems based on patch clearfelling and artificial regeneration. As a consequence, at the beginning of the present century, most Scots pine forests in this region were composed of single-species, densely stocked, even-aged stands. However, towards the end of the twentieth century, the prevailing management regime began to change in two ways. The first involved a greater emphasis on the production of quality pine timber rather than on biomass for pulpwood. The second involved progressive conversion of pure Scots pine stands to mixtures of pine and broadleaves. This latter trend was influenced by both ecological and economic considerations (see Spathelf and Ammer, op cit for more details).

In the state of Brandenburg, since 2004, implementation of the new silvicultural approach has required establishing mixed stands (e.g. MLUL 2016). Therefore, many pure pine stands are currently being converted into mixed forests with a considerable admixture of European beech (*Fagus sylvatica* L.) and oak (*Quercus* spp.). The conversion towards mixed-species stands in public forests has been based on a long-term management approach involving the definition of FDTs to describe the desired future composition and structure of a stand. In the state of Brandenburg, a variety of FDTs have been defined for Scots pine forests. These FDTs can be grouped into those on poor sandy soils where pine is the main tree species and those on soils of medium fertility where significant contents of loam and better water storage capacity would allow pine to be admixed with broadleaved tree species. Silvicultural prescriptions are then developed to cover the management of each FDT (e.g. Fig. 7.1).

Introducing other species into pure Scots pine stands is a comparatively easy task. The shade-tolerant European beech can be planted or sown under fairly dense mature Scots pine stands. Another option for achieving mixed stands of Scots pine and broad-leaved tree species is by underplanting with oak or using oak seedlings regenerating from acorns spread by the European jay (*Garrulus glandarius* L.). In such mixed stands, particularly with European beech, Scots pine needs to be repeatedly released from neighbouring trees by tending and thinning. Final harvesting starts when the pine crop trees have reached their target diameter (40–60 cm dbh depending on region and tree quality). Financial returns (per ha and year) very much depend on productivity of the site and less on the intervention regime. For the best sites, the returns culminate at between 80 and 100 years of stand age at € 150–€ 200 per ha and year. If single pine trees with stems of high timber quality occur, these can be grown on for another rotation.

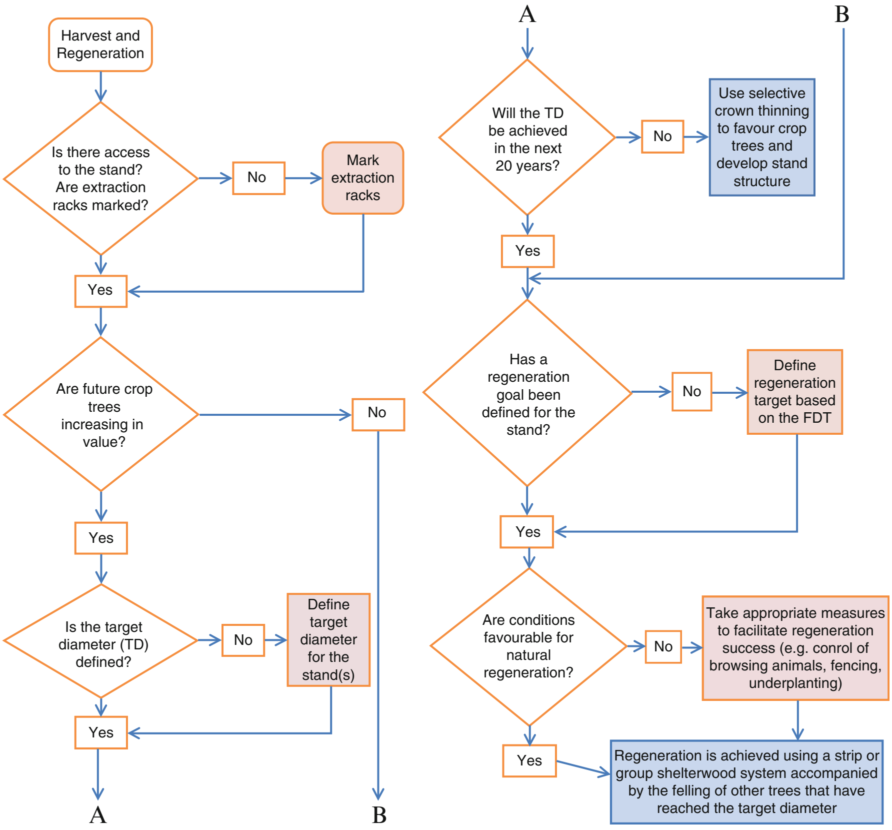

Fig. 7.1 Decision tree outlining the steps involved in the harvest and regeneration processes in a Scots pine-dominated FDT in the German state of Brandenburg. (Adapted from Appendix 3 in MLUL 2016)

Natural regeneration of Scots pine is welcome within the prevailing close-to-nature forest management regime. The success of natural regeneration of pine depends on contact with mineral soil (without accumulation of litter or thick layers of competing herbs), sufficient light and well-controlled ungulate populations. Sometimes thick humus layers or competing vegetation are removed by judicious soil preparation in strips or patches. A variety of silvicultural options exist to regenerate Scots pine, ranging from clear-cuts to group felling or shelterwood systems.

7.2.2 Poland

The Beskid Śląski and Żywiecki Mountains form part of the Western Beskidy Mountains in southern Poland where the elevation ranges between 700 and 1100 masl. During the second half of the nineteenth century, there was large-scale transformation of the natural mixed forests of Norway spruce (*Picea abies* (L.) H. Karst.), European beech and European silver fir (*Abies alba* Mill.) to Norway spruce monocultures. Spruce was favoured because of its relatively fast growth, the production of large volumes of timber with high monetary timber value and ease of management.

By the middle of the twentieth century, it was becoming clear that the site conditions in this mountainous region were not suitable for pure spruce forests. There were many problems with the management of these forests like the increasing impact of wind and snow damage. These difficulties culminated at the beginning of the current century when there was a mass dieback of spruce stands in this region caused by a range of interacting factors including: seed origins used in the nineteenth century were often from the Austrian Alps and proved to be maladapted to the local climate; there were long-term negative impacts of industrial pollutants on soil chemistry and biology; there was widespread damage from *Armillaria* spp. fungi; the forests were increasingly valued for recreation and landscape which resulted in longer rotations and heightened vulnerability to abiotic hazards; and there were more frequent bark beetle outbreaks, partly as a consequence of higher disturbance from drought, wind and snow.

This dieback resulted in the decision to convert the pure spruce stands back to a mixed, structurally heterogeneous and more stable forest type adapted to the local site conditions. The intention is that all silvicultural practices during the conversion process should follow the principles of close-to-nature silviculture (Schutz et al. 2016). The main principles followed in this conversion (Malek 2015) have been as follows: underplanting with seedlings of silver fir and beech (the so-called target species) was carried out in gaps in stands with a light overstorey of surviving spruce; natural regeneration of pioneer species (e.g. Scots pine, birch (*Betula pendula* L.), aspen (*Populus tremula* L.) and European larch (*Larix decidua* Mill.)) would be accepted, while other companion species might be introduced (e.g. lime (*Tilia cordata* Mill.), Norway maple (*Acer platanoides* L.), sycamore (*A. pseudoplatanus* L.), elm (*Ulmus* spp.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco)) to increase species diversity; excessive natural regeneration of Norway spruce would be removed during the tending phase to favour the target species; a range of provenances would be used to ensure adequate genetic diversity; in open areas where spruce stands had disintegrated, nurse trees (e.g. birch, Scots pine) would be introduced for subsequent underplanting with the target species; and the regeneration process would be regularly monitored to ensure satisfactory progress towards restoring a mixed-species forest.

7.2.3 Sweden

In southern Sweden, naturally regenerated oaks (both pedunculate oak *Quercus robur* L. and sessile oak *Q. petraea* (Matt.) Liebl.) are frequently found on favourable sites in different types of mixture with other broadleaves and conifers as well as on nutrient-poor and dry sites in coastal areas of the region (Drössler et al. 2012). In this region there are around 65.000 ha of oak forests (>50% oak by basal area), but a considerable additional proportion of oak occurs as scattered trees in pastures and as mixtures with other tree species in forests (Almgren et al. 1984; Swedish Forest Agency 2014). Common mixtures are oak/Norway spruce and oak/Scots pine with or without other broadleaf species, such as birch, aspen, beech and lime. There are also broadleaved mixtures of oak and other broadleaf species. Many of these pure oak or oak-rich mixed forests derive from historical land uses such as woodland pasture, coppice woodland or, more recently, abandoned fields and pasture, and most are owned by small private forest owners (Löf et al. 2016).

The idea of managing such naturally regenerated mixed stands with the main aim of producing oak timber was developed by a local forest manager in Blekinge, south-eastern part of Sweden (Ståål 1986). No experimental data exist for this type of management, but several plots have been monitored for a period of more than 60 years. The system relies on there being abundant natural regeneration of oak, and the practicality of implementing it is determined by an inventory carried out before a stand reaches 30–40 years of age. At this stage, there should normally be about 10% of oaks in the stand, while the rest can be a variable mixture consisting of both broadleaved and coniferous tree species. The objective of the monitoring is to determine if there are enough young oaks that can be developed into timber trees, i.e. a minimum of 40 evenly spaced future crop trees per hectare at the end of the rotation (ca 120 years). If these conditions are met, future oak crop trees are marked and managed individually for the rest of the rotation. Individual management of future crop trees includes pruning of crop trees up to ca 7–8 m if necessary. Thinning of the stands is done relatively often (i.e. every 5 years) in the initial decades and less frequently (i.e. every 10–15 years) as the stand ages. The whole stand is thinned, and all types of tree are harvested, but the thinning pattern applied ensures that the crowns of the future oak crop trees are released. Any subdominant or understory tree species near the oaks are preserved. By the end of the rotation, the proportion of oaks relative to other tree species will have increased. Although this system involves a long rotation, the management is considered cost-effective due to the limited investment in the early years with reliance upon natural regeneration and because most thinning operations yield a surplus since they are applied from the middle of the rotation onwards with a higher average tree size.

7.2.4 United Kingdom

At the beginning of the last century, the forest area of the United Kingdom (UK) had been reduced to around 5% of the land area as a result of centuries of uncontrolled timber exploitation, overgrazing and conversion to agriculture. The implementation of a sustained programme of afforestation, primarily of marginal agricultural land in upland areas, increased the proportion of forest to 13% of the land surface by the early years of the present century. These ‘new’ forests were mainly composed of conifers, often of non-native species such as Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and were typically single-species even-aged plantations (Mason 2007). In

Table 7.1 Species composition and productivity of the more heavily thinned plot in a 'diversification' experiment in Wykeham Forest, north England, 63 years after the enrichment planting of a pure Scots pine stand with 27 different tree species

Species	Trees (>7 cm dbh) ha^{-1}	Top height (m)	Mean dbh (cm)	Basal area (m^2 ha^{-1})
Pinus sylvestris	97	23.3	36.9	10.5
Abies spp. [a]	161	30.0	16.8	6.7
Larix spp.	40	27.1	37.5	5.3
Tsuga heterophylla	180	16.9	12.3	2.4
Other conifers [b]	43	19.2	20.5	3.2
Betula spp. [c]	102	19.7	18.7	3.2
Quercus spp. [d]	70	23.0	19.5	2.4
Fagus sylvatica	37	24.2	24.5	1.9

[a] *Abies grandis*, *A. procera* and *A. veitchii*
[b] *Cryptomeria japonica*, *Picea omorika*, *P. sitchensis*
[c] *Betula lenta*, *B. lutea*, *B. pendula*
[d] *Quercus petraea*, *Q. robur*, *Q. rubra*

general, pine species were favoured in afforestation of sites on the drier eastern side of Great Britain, while the more productive spruces, Douglas fir and silver firs were preferred in more oceanic climate of western Britain. From the middle of the last century, there was interest in trying to diversify the species composition of these conifer forests, partly for ecological reasons, but also to try to improve their productivity (Zehetmayr 1960).

One study relevant to the theme of this chapter was a trial established in 1950 in a 22-year-old Scots pine stand on an iron pan soil in north-east England. This was designed to monitor the potential and performance of 27 alternative native and non-native species (16 conifers and 9 broadleaves) planted along cultivated rows cut through the pines when the latter were about 3 m tall (Mason 2006). Twenty-five years later, only three species had failed to survive and six conifers were of equivalent height to the 'nurse' pines. In the 1990s, two plots were established in this trial with differential thinning regimes introduced to favour the best quality stems irrespective of species while providing a light environment that would allow satisfactory growth of naturally regenerated seedlings. Sixty-three years after the start of the trial, in the more heavily thinned plot, the Scots pine component accounted for only 13% of the trees and 29% of the basal area (Table 7.1). Extensive natural regeneration of the more shade-tolerant western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and silver fir species had meant that they now comprised 23% and 21%, respectively, of the trees, despite a rather low proportion of the total basal area because of the presence of numerous small stems of these species in the lower canopy. Furthermore this previously pure Scots pine stand now contained 32% broadleaved trees by number. However, the success of this experiment was not repeated in similar trials installed in spruce plantations on moisture peaty gley soils elsewhere in upland Britain (Stewart 1960). Here the faster growth of the spruce matrix and severe browsing damage by roe deer (*Capreolus capreolus*) detrimentally affected survival of the interplanted species, while the higher risk of windthrow on these exposed sites limited the feasibility of thinning to release any surviving trees in the understorey (Forest Research, unpublished data).

Other information relevant to the development of mixtures in plantation forests is provided by two long-term trials in Scotland investigating the transformation of even-aged stands (Kerr et al. 2010; Cameron and Prentice 2016). Both these trials were established in the early 1950s with the aim of transforming even-aged conifer stands composed of species such as Douglas fir, Norway spruce, larches and Scots pine to irregular structures of mixed-species composition. In one of the sites, the aim was to create an irregular forest composed of Norway spruce, European silver fir and beech (Kerr et al. 2010). At both sites the transformation process was started by cutting small gaps (initially 0.01–0.02 ha but subsequently 0.1–0.2 ha) in the stand and planting these with the desired species. As time progressed, the increased frequency of natural regeneration meant that there was less need for planting gaps (Cameron and Prentice 2016). Recent surveys showed a progressive decline in the incidence of light demanding species and regeneration largely dominated by more shade tolerant species. Thus at Glentress, pines and larches had declined from over 70% of trees in 1952 to around 25% in 2010: over the same period the proportion of spruces had risen from just under 20% to nearly 68% (MacKintosh et al. 2013). There were also slight increases in the occurrence of more shade tolerant species (e.g. western hemlock, red cedar (*Thuja plicata* D. Don.), grand fir (*Abies grandis* (D. Don) Lindl.), European beech). Similarly, at Faskally, the numbers of Scots pine and European larch seedlings are only around 10% of those of more shade tolerant species (Cameron and Prentice 2016, their Table 3). It remains unclear where the increasing incidence of shade tolerant species will result in the progressive elimination of valuable species of intermediate shade tolerance such as Douglas fir. Browsing pressure from deer and sheep has also influenced the development of these mixed stands since species such as European silver fir and beech were preferentially browsed and have proved difficult to establish (Kerr et al. 2010).

7.3 Synthesis of Case Studies and Role of FDTs

Although necessarily limited in number and regional coverage, there are some common themes emerging from these case studies. The first is that successful development of mixtures requires species being planted or regeneration occurring in either the early stand initiation phase or in the understorey reinitiation phase (terminology of stand development follows Oliver and Larson 1996). Thus in the UK and in Poland (after collapse of the previous Norway spruce stand), species diversification was achieved by planting in gaps that are deliberately created or under a young shelter of pioneer species. In Sweden, the development of oak in mixture with a range of species was also a result of regeneration in the stand initiation phase, although formal development relied upon structured thinning in the stem exclusion phase. By contrast, in Germany and in Poland, the introduction of shade tolerant species such as beech and European silver fir, took place in older stands where the canopy of mature trees had opened up sufficiently (either through thinning or mortality) to allow the survival and growth of underplanted seedlings or regeneration.

A second theme is that the fostering of mixtures in the case studies generally resulted in the move away from stands dominated by light demanding species to one in which shade tolerant species begin to dominate (Germany, UK). The possibility of maintaining a light demanding species such as Scots pine may require special measures such as clear felling of larger gaps and/or site cultivation to provide a favourable seed bed. The third point consequent upon the above is that it can take several decades to successfully develop a mixed stand and careful tending was often necessary during the regeneration phase to ensure that the future mixed stand develops along the planned trajectory. It was apparent in most studies that most admixed species were vulnerable to browsing by deer and other ungulates with the risk that such pressure can result in the eventual species composition being other than intended.

One point emerging from these case studies, as well as from the country reports (Mason et al. 2016), is the utility of concepts such as forest development types (FDTs) to guide managers in identifying the desired species composition of the mixtures that they are trying to create. Examination of the British case studies reveals little evidence of a clear goal in terms of the eventual species mixture, whereas in both Germany and Poland, it is evident that the ultimate target is defined in best practice silvicultural guidelines. However, as noted above, only a few European countries indicated that FDTs were available to guide mixture development, and there is relatively little description of the role of FDTs in the literature (but see Witt et al. 2013; Wilson 2016). The most comprehensive description is that provided by Larsen and Nielsen (2007) where they state:

> A FDT describes the long-term goal for forest development on a given locality (climate and soil conditions) in order to achieve specific long-term goals [. . .] The FDT will serve as a guide for future silvicultural activities in order to 'channel' the actual forest stand in the desired direction. (pp. 109–110)

Thus the key point is that FDTs integrate information about the tree species that are adapted to particular sites to identify those that can be favoured by management and their proportional representation in the future stand. As shown by Larsen and Nielsen (op cit), the FDTs can be a mixture of native and non-native species and can be used to indicate the proportion of the main species to be found in the type as well as the species that could be minor components of the future stand. The preparation of FDTs can also provide a means of guiding local managers on the potential mixture options that are suited to their sites and conditions. Although the overall number of FDTs can vary considerably (e.g. 19 in Denmark (Larsen and Nielsen 2007) and 39 in the German state of Lower Saxony (Spathelf et al. 2016a)), in practice, the number that is applicable to a particular site or region is likely to be relatively limited.

7.4 Using FDTs to Develop Silvicultural Guidelines for Mixed Forests

We suggest that the framework provided by the FDT concept represents a structured means to devise guidelines for mixed forests that can avoid the generality associated with many forest policy statements promoting the wider use of mixtures, while still providing flexibility for silvicultural innovation at a local level and avoiding the rigidity associated with traditional top-down prescriptions for forest management (Larsen and Nielsen 2007; Lawrence 2017). While the FDT structure can be developed at a national or regional level to produce a series of types, the process can also be applied in a more informal way by a forest manager or owner to provide a coherent silvicultural strategy for the management of a range of site types found within their property. Although development of FDTs should be easier if dealing with native species whose ecological requirements are well understood, the approach can also be used with non-native trees and can serve to integrate the latter into mixed forests. In addition, the frame of one or more FDTs can be used to classify existing or proposed experimental trials and plots so that the information produced is more readily transferred to forest managers. FDTs also provide a means of structuring the often complex outputs from scenario analysis based on growth models to provide useful guidance to managers on appropriate ways to manipulate mixed forest stands (Pretzsch and Zenner 2017).

For a given forest, or a site within that forest, the process would begin by identifying those species which are suited to the edaphic characteristics of that site. The increasing availability of decision support systems (DSS) which combine site features (soil nutrients and soil moisture) with knowledge of individual species' ecological niches (e.g. Ecological Site Classification in the UK – Pyatt et al. 2001; Fichier Ecologique des Essences in Belgium – Claessens et al. 2014) can be used to classify the potential suitable species. Such classifications frequently distinguish four levels of suitability of a species ranging from 'optimum' or 'suitable' where a species can be expected to grow well on a site or with some constraints, through 'marginal' where a species can grow but only as a 'minor' component of a stand to 'unsuitable' where a species is not suited to a site. A species would have to be classed in the first two categories of suitability to be potentially considered as a 'major' species in the future stand. One advantage of these DSS is that they can be combined with projected changes in temperature or precipitation to indicate likely sensitivity of a species on a given site to projected climate change and to identify possible alternatives (e.g. Witt et al. 2013; Ray et al. 2014). They can also be used to evaluate the potential sensitivity of native species to climate change and to explore the possibility that individual components of an existing association may be differentially affected by climate change (Kirby 2013).

Once the candidate 'major' and 'minor' species have been identified, their potential utility should be examined in the light of the objectives set for the forest or property. For instance, the potential species combinations to be used may differ if the primary objective is to provide industrial timber for a nearby mill, compared to a situation where recreation and wildlife conservation feature highly in the aims of management. After the species have been ranked for their compatibility with the objectives, their individual functional traits (e.g. shade tolerance, rooting pattern, early growth rate, nutritional aspects) should be carefully reviewed to see how these might affect their performance when grown in mixture. In this way, one can ensure that the silvicultural treatments applied to any mixture reflect the management objectives chosen for the forest while respecting edaphic factors and species composition and characteristics.

Given that the species are suited to a particular site (see above), then the two characteristics that are most likely to influence species compatibility are the rate of height growth over time and the shade tolerance of the individual species (Bauhus et al. 2017). An example of the way species growth rate and shade tolerance might influence performance in mixture is provided by comparing the outcome when Norway spruce and birch are grown in mixture in north-west Europe compared with results when Sitka spruce is admixed with birch in Britain. In the first instance, the slower early height growth of Norway spruce and its relatively high shade tolerance can result in the formation of two-storied stands where the spruce grows underneath the birch (Frivold and Groven 1996). However, in the second case, the appreciably faster early growth of Sitka spruce and its lesser shade tolerance mean that at the beginning of canopy closure, trees of the two species are of a similar height and are competing for light, and so a two-storied mixture is not attainable. The end result is that the greater height attained by the Sitka will result in the light-demanding birch being shaded out and the eventual formation of a pure spruce stand (Humphrey et al. 1998).

In general, the more shade intolerant a species, the more it will require to be growing in the upper canopy if it is not to be shaded out in mixture (Bauhus et al. 2017). Alternatively, such a species should be grown in discreet patches (‘mosaics’) which are large enough to allow sufficient crown development for at least one tree to reach maturity (Spiecker 2006). Thus consideration of important functional traits can provide useful information as to the pattern of mixture (e.g. tree by tree, line by line, group) that is likely to be most effective in ensuring the persistence of the admixed species over time (del Rio et al. 2015). In practical terms, it is a mistake to propose a complicated pattern of mixture within a given FDT in the hope that this will be maintained by future thinnings. A more realistic approach is to define a FDT as having one or two major species accounting for perhaps 50–70% of the stand, screened for potential vulnerability to climate change, admixed according to their functional characteristics and complemented by a number of minor species which might each occupy 5–10% of the stand. It follows that once a FDT is defined, appropriate silvicultural regimes can be proposed based on the characteristics of the major species. For example, in the Danish FDT of Sitka spruce with pine and broadleaves (Larsen and Nielsen 2007), the light demanding to intermediate shade tolerance of the pine and the spruce elements of the mixture would suggest that the pattern of mixture should be in groups and that regeneration could be achieved through a group or irregular shelterwood system. Similarly, Fig. 7.1 shows how key silvicultural prescriptions for the harvesting and regeneration of Scots pine-dominated forests in Brandenburg can be codified within the framework of a FDT.

7.5 Conclusion

Increasing tree species diversity in forests through the creation of more mixed stands is a common aim of forest policies in different parts of the world, both as a means of increasing the delivery of ecosystem services from forests and as a way of increasing resilience to climate change. However, it is clear that forest managers charged with implementing a strategy of 'diversification through mixture' can find the task challenging, not least because successful implementation of the strategy may take decades and there is often a lack of silvicultural guidance about how best to proceed (Lawrence 2017). The silvicultural approaches for managing mixed forests are often more complicated than those used in even-aged, single species stands, and a lack of experience of the appropriate silviculture can discourage uptake of alternative measures (Puettmann et al. 2015). In such situations, there is a major need to produce silvicultural guidelines that simplify the generalities often characteristic of policy aspirations into practical measures that can be delivered in the field and over time, possibly by a succession of managers. Key to this simplification is to structure silvicultural proposals through the definition of an appropriate number of FDTs that are adapted to local conditions and which are robust to the impacts of future climate change (i.e. dynamic FDTs). In order to incorporate the impacts of future climate change in current silvicultural decisions, site parameters which are crucial for tree species growth (e.g. soil water deficit during the growing season) have to be forecast. For example, Spathelf et al. (2016b) modelled the probabilities of the economically most important tree species in the German federal state of Brandenburg to grow on a given site in the years 2055 and 2095. This approach can facilitate decisions about where to concentrate conversion activities from even-aged pure conifer (Scots pine) forests to mixed broadleaved forests.

Within an extensive forest holding (e.g. a state forest service), different FDTs can be located in space using GIS (Witt et al. 2013), the progress of the existing forest towards the desired future condition(s) can be monitored and changes made as required. When placed within the framework of a FDT, the provision of silvicultural guidelines can provide a specific and site-sensitive long-term vision for the development of a mixed forest, ultimately as a means of adapting a forest to the biophysical challenges of the present century.

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Chapter 8
Silviculture of Temperate Mixed Forests from South America

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Abstract Temperate mixed forests of South America extend mostly from 33°S to 55°S latitude and between the Pacific Ocean and the Patagonian Steppe east of the Andes Mountains. West of the Andes in Chile, in a high precipitation regime, the most diverse and large forest types develop. These forests simplify in composition and structure toward the south due to reductions in temperature and in a more pronounced manner east of the Andes, in Argentina, because of an abrupt reduction of the precipitations. Descriptions of the main temperate mixed forest types of Chile and Argentina are presented, focusing on ecologic issues and management proposals. For Chile, we address in this chapter secondary and old-growth forests of the evergreen forest type and secondary forest dominated by *Nothofagus* spp. For

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Argentina, we discuss the case of mixed *Nothofagus* spp. forests in the old-growth phase and of *N. dombeyi* and *Austrocedrus chilensis* mixed forests in the transition from the mesic to the xeric zone. There is a strong ecological and silvicultural base knowledge for the sustainable management of these mixed forests. However, with a few exceptions, its broad application is a pendant matter in both countries.

8.1 Introduction

In South America, temperate forests occur between 33°S and 55°S latitude, at the southernmost tip of the continent (Fig. 8.1). They represent a biogeographic isolated forest island, surrounded by different physionomic and taxonomic types of vegetation (Armesto et al. 1997). The composition and distribution of these forests are regulated by environmental longitudinal and latitudinal gradients. The strong W-E precipitation gradient is mostly due to the Coastal Mountain range in Chile and the Andes Mountain range between Chile and Argentina, both acting as obstacles for the humid winds coming from the Pacific Ocean. The climate is characterized for its moderate to low temperatures that decrease with latitude. Precipitation increases progressively from north to south, being below 300 mm year^{-1} in the so-called Mediterranean region in Chile, above 35°S, and 3000–5000 mm year^{-1} on the western slopes of the Coastal and Andes Mountains south of 38°S, where humid air masses come from the Pacific Ocean. East of the Coastal Mountains in the intermediate depression (40°S), the precipitation diminishes to 2000 mm year^{-1}. On the rain shadow of the Andes, 50 km east from them, precipitation drops dramatically down to around 500 mm year^{-1} in the ecotonal area between the forest

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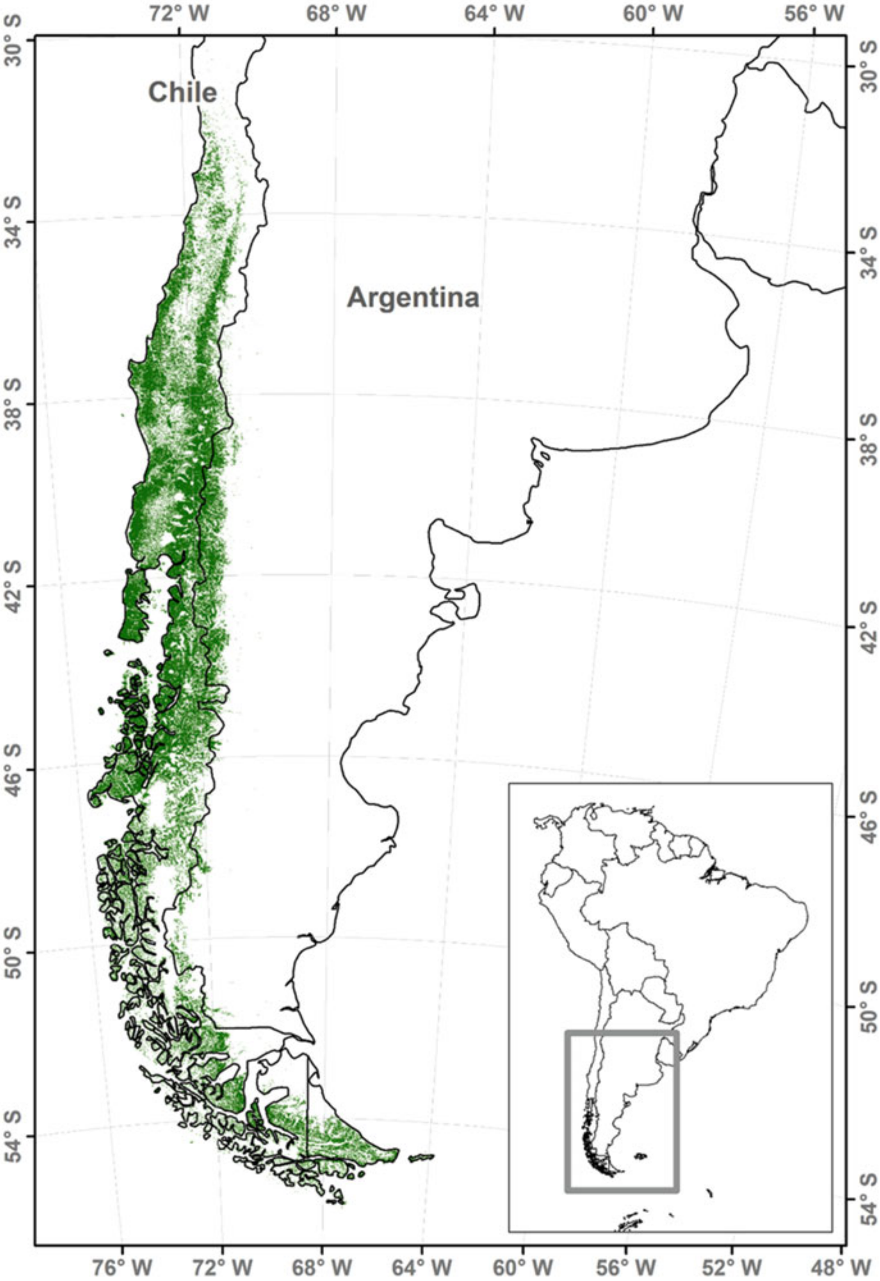

Fig. 8.1 Map of temperate forest of South America from Chile and Argentina. (Extracted from Hansen et al. 2013)

and the steppe and faster east continue to decrease in the Patagonian steppe. Most of this ecotone territory is located within the Argentinean borders, but farther south part of it falls within Chilean territory. These precipitation differences result in the occurrence of mixed and pure forests with high diversity of species, mainly west of the Andes in Chile, north of 47°S. Toward the south, forest composition and structure become simpler, mainly east of the Andes, in North Patagonia, Argentina (Veblen and Alaback 1995). Glaciers have modeled the landscape, and most soils are volcanic, originated from recent andesitic volcanic ashes.

Several forest types are found in the region. West of the Andes, in Chile, between 33°S and 37°S, there is the Mediterranean sclerophyll forest, and between 37°25′S and 43°20′S, it is found a temperate rain forests called Valdivian. Between 43°20′S and 47°30′S, there is the Nord Patagonian rain forest, and further south the Magellanic rain forest occurs (Veblen and Alaback 1995). At relatively high elevations along the whole region, pure *Nothofagus pumilio* subalpine forests are present, and low *N. antarctica* forests occur on a variety of sites, mainly on those poorly drained, cold valley bottoms and the ecotone. East of the Andes, in Argentina, along the strong precipitation gradient between 37°30′S and 55°S, the Patagonian Andes or subantarctic *Nothofagus* forests are found. They are mainly pure stands of *Nothofagus* spp., dry forests, and woodlands, limiting with grasslands and bushes of the Patagonian steppe (Veblen et al. 1996).

Different natural disturbances, such as volcanism, earthquakes, landslides, snow avalanches (in Chile), and wildfires, massive bamboo flowering, and windstorms (in Chile and Argentina), have modeled these forest ecosystems (González et al. 2014). However, the distribution and current structure of the forest types have been strongly affected by anthropogenic fires since the middle 1800s, mainly during the European settlement, because fire was used as a tool to transform forests into agricultural and cattle-raising land (Willis 1914; Otero 2006). During the last century, part of the forest regenerated naturally as secondary (Lara et al. 2003; Veblen et al. 2003). In Magallanes and Tierra del Fuego (47–55°S), wind blowdown is the main disturbance (Rebertus et al. 1997).

Forests are more mixed west of the Andes, in Chile. The most diverse species community forests occur in the dry north, between 37 and 38°S (Bannister et al. 2012), but the evergreen forest, located between 38°S and 47°S, holds the greatest tree species richness (Donoso et al. 1998; Donoso 2015). Half of the 13.6 million ha of Chilean native forests are mixed. The largest broadleaf pure forest types are *Nothofagus pumilio* and *Nothofagus betuloides* (despite the ecotone both species grow together). The conifer forests are *Fitzroya cupressoides*, *Araucaria araucana*, *Pilgerodendron uviferum*, and *Austrocedrus chilensis*, although they form mixed stands on certain sites. Among the Chilean 6.84 M ha of mixed forests, the main types are evergreen (4.13 M), *Nothofagus obliqua-N. nervosa-N. dombeyi* (1.47 M), *N. dombeyi-N. nervosa-Laureliopsis philippiana* (0.56 M), Mediterranean sclerophyll (0.47 M), and *N. obliqua-N. glauca* (0.21 M) (CONAF 2013).

East of the Andes, in Argentina, 95% of the 3.29 M ha of temperate forests are pure (CIEFAP-MAyDS 2016). The *N. pumilio* and *N. antarctica* forests stand out from the rest because they occur along the whole latitudinal range (37–55°S). Up north, *A. araucana* coniferous forest occurs at medium latitudes, *N. dombeyi* grows on mesic sites, and the *Austrocedrus chilensis* forest occurs on mesic as well as on xeric environments. These three species grow in monospecific as well as in two-species stands, with low participation of one of them (<20% of the canopy cover), covering 427,000 ha (CIEFAP-MAyDS 2016). Mixed forests add up to 284,000 ha, and they are defined as those composed by two or more species, given that none of them provides more than 80% of the canopy cover (Bravo-Oviedo et al. 2014). Evergreen and mixed *Nothofagus* stands are basically mixed ingression forests coming from the western side of the Andes were they prosper. There are also mixed post-fire woodlands of forest sprouting species like *N. antarctica*, *Lomatia hirsuta*, *Schinus patagonicus*, and *Maytenus boaria*, which are seral stages of the high *A. chilensis* and/or *N. dombeyi* forests (Veblen et al. 1996; Kitzberger 2012; Rusch et al. 2016). There is also mixed forest of *A. araucana-N. pumilio* and other in small areas with other tree species combinations, such as *A. araucana-N. antarctica* and *A. chilensis-N. obliqua*. The composition of the mixed stands located among the pure depends mainly on the type of disturbance that originated the stand, climatic conditions during the establishment period and species growth rates within the niche (Kitzberger 2012; González et al. 2014).

In Chile, most adult forests are mixed, as well as 3 M ha of secondary forests, and thus mixed stand silviculture should be the essential tool to apply (Donoso et al. 1993b, c; Lusk and Ortega 2003). Secondary forests can be managed focusing on one, two, or several strata, which imply getting involved into uneven-age management or multiage silviculture (Nyland 2003; Donoso 2013). Encouraging mixed forest silviculture is crucial for ecosystem conservation, and since these forests are highly productive, social and economic benefits can be expected as well (Donoso 2015).

In Argentina, silviculture has been developed mainly for the dominant species of each forest type (Bava 1999; Loguercio 1997; Loguercio et al. 2018; Martinez Pastur et al. 2013; Peri et al. 2016), with the exception of the mixed *Nothofagus nervosa-N. obliqua-N. dombeyi* forest type at Lanín National Park, at 40°S, (González Peñalba et al. 2016; Sola et al. 2015). However, east of the Andes, mixed forest management should be given more attention considering that since environmental resources are limited, forests are more susceptible to climate change effects, which render stand adaptation and resilience as two main subjects.

Hereafter, the state of the art of the silvics of four mixed forest types of the region is presented, two of them for the rain forest, west of the Andes, and the other two for mesic-xeric sites, east of that range. On the rain forest, old-growth evergreen stands are proposed to manage it as multiaged, and secondary forests have been managed as even-age with one or two strata. On a mixed *Nothofagus* forest, tending cuttings have been applied at the stem exclusion stage (sensu Oliver and Larson 1996), in stands with and without shade-tolerant species in the understory. On the eastern side of the Andes, on even-aged mixed *Nothofagus* forests, a shelterwood system has been applied, and at last pure *A. chilensis* stands with the presence of *N. dombeyi* regeneration are being converted into a mixed *N. dombeyi-A. chilensis* forests.

8.2 Evergreen Forests

8.2.1 Distribution and Ecology

The so-called evergreen forest type (EFT) is the largest in Chile (4.3 million ha; www.sit.conaf.cl). The EFT is comprised of a great variety of community types having two common characteristics: (1) the dominance of a variable number of evergreen species, including some Podocarpaceae conifers, and (2) their occurrence under a climate of high pluvial precipitations throughout the year (Donoso 2015). It is present from 38° to 47°S in Chile, mostly concentrated in the Coastal Cordillera, the western slope of the Andean Cordillera, and the Island of Chiloe (Fig. 8.1), where forests have the potential for management, but also in the northern portion of the archipelago. They grow below 1000 m a.s.l. in the northernmost latitudes and at elevations of less than 300 m in the southernmost latitudes. The ample geographical range where this forest type develops implies a variation in temperature and precipitation from north to south, in addition to many variations in site fertility. Andean forests are affected by large-scale disturbances (landslides, fires due to volcanic eruptions, etc.), while forest dynamics in the Coastal range is shaped by small-scale disturbances (e.g., windthrow and canopy gaps) (Veblen 1985; Veblen et al. 1981). Soils in the Andes are of medium to high fertility, while in the Coastal range they are of poor fertility (CIREN 2001), but better at lower elevations (Donoso and Nyland 2005).

The EFT has this name because all tree species, mostly hardwoods, are evergreen. These species are listed in Table 8.1, including some life history traits. Long-lived pioneers may reach emergent positions (40–50+ m; Parada et al. 2003) in mature or old-growth forests, such a *Nothofagus dombeyi*, *N. nitida*, *Weinmannia trichosperma*, and *Eucryphia cordifolia*. Canopy species (25–35 m) include two conifers (*Saxegothaea conspicua* and *Podocarpus nubigena*, although also *Podocarpus nubigena* may be found at lower elevations) and *Laureliopsis philippiana*, *Dassyphyllum diacanthoides*, *Drimys winteri*, *Aextoxicon punctatum*, and *Persea lingue*. Lower canopy tree species (<20 m) include mostly those of the Myrtaceae family (*Amomyrtus luma*, *Amomyrtus meli*, *Luma apiculata*, *Myrceugenia planipes*), of the Proteaceae family (*Lomatia ferruginea*, *Lomatia dentata*, *Gevuina avellana*, and *Lomatia hirsute*), and *Caldcluvia paniculata*. Some of the mentioned Proteaceae plus *Embothrium coccineum* can act as pioneers as well, but they are relatively short-lived (Table 8.1). Overall, this forest type can have more than 20 tree species in a single forest stand, but of course, this is highly variable according to site productivity that is determined by geographical location.

Table 8.1 Main tree species of the evergreen forest type and some of their life history traits

Species	Family	Life-span[a]	Tolerance to shade	Soil fertility requirements
Nothofagus dombeyi	Nothofagaceae	Long	Intolerant	Low
Nothofagus nitida	Nothofagaceae	Long	Midtolerant	Low
Weinmannia trichosperma	Cunoniaceae	Long	Intolerant	Low
Eucryphia cordifolia	Cunoniaceae	Long	Midtolerant	Medium
Laureliopsis philippiana	Monimiaceae	Long	Tolerant	High
Dassyphyllum diacanthoides	Compositae	Long	Midtolerant	Medium
Saxegothaea conspicua	Podocarpaceae	Long	Midtolerant	Medium
Podocarpus nubigena	Podocarpaceae	Long	Tolerant	Low
Podocarpus salignus	Podocarpaceae	Long	Midtolerant	High
Drimys winteri	Winteraceae	Medium	Midtolerant	Low
Aextoxicon punctatum	Aextoxicaceae	Long	Tolerant	High
Persea lingue	Lauraceae	Long	Tolerant	High
Amomyrtis luma	Myrtaceae	Long	Tolerant	Medium
Amomyrtus meli	Myrtaceae	Long	Tolerant	Medium
Luma apiculata	Myrtaceae	Medium	Tolerant	Medium
Myrceugenia planipes	Myrtaceae	Medium	Tolerant	Low
Caldcluvia paniculata	Cunoniaceae	Short	Midtolerant	High
Embothrium coccineum	Proteaceae	Short	Intolerant	Low
Lomatia ferruginea	Proteaceae	Short	Midtolerant	High
Lomatia dentata	Proteaceae	Short	Tolerant	Medium
Lomatia hirsute	Proteaceae	Short	Intolerant	Low
Gevuina avellana	Proteaceae	Short	Intolerant	Low

References: Donoso (2015), Lusk et al. (1997), and Gutiérrez and Huth (2012)
[a] Long >200 years, medium 100–200 years, short <100 years

8.2.2 *Silviculture in Secondary Forests*

Even-aged secondary forests are dominant in most regions at low and medium elevations in south-central Chile, where past fires for land conversion to agriculture were common, sometimes combined with selective harvesting (Otero 2006; González et al. 2015), leading to open areas that were invaded by pioneer tree species or by a mixture of tree species. In the ample region of the EFT, it is possible to find a variety of secondary forest, but the most common are those dominated by pioneer species such as *N. dombeyi* or by *D. winteri*, but secondary forests dominated by *W. trichosperma* or by *E. cordifolia* may also occur. However, it is also very common to find secondary forests that are a mixture of species of different shade tolerances that have developed following selective harvesting and fires

Fig. 8.2 Different types of common secondary forests within the EFT. (**a**) *Drimys winteri*; (**b**) *Eucryphia cordifolia*; (**c**) *Nothofagus dombeyi*; (**d**) *Mixed*. (Photographs P Donoso)

(González et al. 2015). Some are shown in Fig. 8.2 and typical diameter frequency distributions represented in Fig. 8.3. Although some of these secondary forests are clearly dominated by pioneer species, all correspond to a mixture of tree species. The degree of species mixture in these secondary forests may also be determined by the successional stage of the forest, with a greater likelihood of increasing mixture in stands in the "understory reinitiation stage," as compared to stands in the "stem exclusion stage" of stand dynamics (sensu Oliver and Larson 1996).

These secondary forests in Chile are now on average between 60 and 100 years (e.g., González et al. 2015), passed the age of fastest growth for individual trees (during the two or three first decades of development in initially dense secondary forests), but are experiencing high productivity rates (as high as 15–20 m^3 ha^{-1} $year^{-1}$ Donoso et al. 1999; Navarro et al. 2011), although on average closer to 8–10 m^3 ha^{-1} $year^{-1}$ (Donoso 2015). One major question is whether mixed-species secondary forests are more productive than their analogue pure species secondary forests, but the additive basal area reported by Lusk and Ortega (2003) for mixed-species *Nothofagus*-dominated secondary forests suggests that additive productivity might also occur in these mixed-species forests. In any case, foresters should manage them accordingly. This however depends on whether the expected silvicultural system is for an even-aged one-stratum forest or for a two-stratum forest (even-aged or two-aged) or converted to an uneven-aged forest. In this section we will provide examples of secondary forests managed as even-aged one- or two-stratum forests, with examples for mixed-species forests and for *D. winteri*-dominated forests in the stem exclusion stage. The case of *N. dombeyi*-dominated forests within the evergreen forest type is also interesting, but since it is given in another section of this chapter, we will not deal with it here.

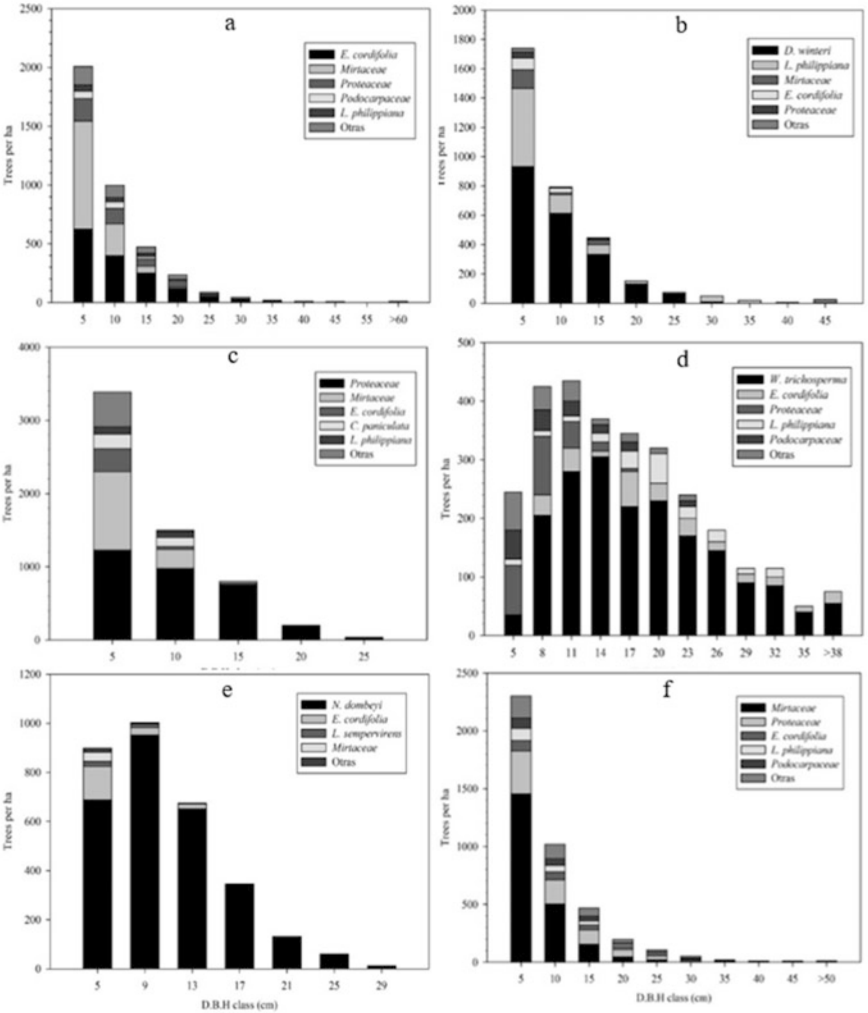

Fig. 8.3 Representation of the diameter frequency distributions of six different mixed-species secondary forests dominated by different species that belong to the EFT. (**a**) *E. cordifolia*; (**b**) *D. winteri*; (**c**) *E. coccineum*; (**d**) *W. trichosperma*; (**e**) *N. dombeyi*; (**f**) Mixed. The lower limit for each diameter class is shown, but notice that they are variable (from 3 to 5 cm). Also the y-axes vary due to the great differences in numbers of trees among some stands

8.2.2.1 Mixed-Species Evergreen Forest

Mixed-species evergreen forest is the result of a mixture of regeneration strategies from propagules in a forest stand, including stump and root sprouts, advanced regeneration, and buried or newly dispersed seeds. As a consequence, these forests have short- and long-lived pioneer species (shade-intolerant and midtolerant), canopy species (midtolerant or shade-tolerant species), and mostly low canopy shade-tolerant species. These forests can include most of the species mentioned in Table 8.1. Here we present two cases, one for forest located at 400 m a.s.l. in the Coastal range at 40°S (Llancahue; Fig. 8.3f) and another at 450 m a.s.l. in the Andes range at 42°S (Correntoso; Fig. 8.3c). The forest in Llancahue is 70 years old (González et al. 2015) and that in Correntoso 26 years old (Schlegel 2014), both in the stem exclusion stage. Both forests have a high proportion of their tree density and basal area concentrated in Proteaceae species (*G. avellana* in Llancahue and *E. coccineum* in Correntoso), in addition to a mixture of midtolerant and shade-tolerant species. In Correntoso *E. coccineum* is going through an accelerating process of mortality and declining diameter growth (6 mm after reaching 10 mm per year at age 10–15, while the remaining tree species have been increasing their growth rates until reaching a plateau of 8 mm during the last years) (Schlegel 2014). While in the Llancahue forest tree species likely have a slow growth rate, there is no evidence of a major mortality of *G. avellana*. Anyhow stand development has been slower in Llancahue, with similar numbers of trees as Correntoso (close to 4000/ha), although a greater basal area (63 vs. 42 m^2 ha^{-1}).

These two cases illustrate that mixed-species secondary forests in the EFT may need early cleaning operations to reduce competition of pioneer species of rapid growth but little potential commercial value, or otherwise an early first thinning that would be mostly precommercial, unless there is a chance to use or sell some firewood. What is important in any case is that tree density must be reduced quite early to allow valuable species to have relatively high diameter rates.

In addition to defining the means to control density and composition in these types of dense and mixed forests, the challenge is to define the intensity and periodicity of future thinnings to reach a desired final mean diameter. To lower tree densities to an average of 400 trees per hectare with a mean diameter close to 35 cm at the time of final harvest, there should be probably three or four thinnings. Density control should be conducted within management zones defined by residual (after thinnings) and maximum (before thinnings) densities estimated through size-density equations or stand density diagrams (Nyland 2002).

In the case of managing only for the canopy-dominant species, for a one-story forest, most favored tree species of high potential commercial value would include some midtolerant or shade-intolerant species (Table 8.1). Therefore, these mixed forests could be managed for two or three major tree species of relatively fast growth rates if density is continuously controlled. In the case of managing for two strata, the second stratum would include mostly midtolerant and shade-tolerant species.

In these examples, following the early density control of non-valuable pioneer species, for the one-stratum management, selected species should be favored by successive crown thinnings. The starting point in these mixed stands with no previous interventions would be usually a relative density above 80% (Schlegel 2014; Donoso et al. 2014b). Considering that mortality is severe above 80% relative density in hardwoods (Nyland 2002) and thinning regimes have to balance good growth rates of individual trees with adequate stockings at the stand level for good volume growth rates, the management zone for these stands could range from 40% to 60% (but see section for *D. winteri* forests).

It could be expected that future diameter growth in these managed forests should be around 0.5 mm per year (Schlegel 2014; Navarro et al. 2017), although they may be lower if there is no early control of tree density. To reach an expected mean diameter of 35 cm for the rotation age, the time remaining would be approximately 30–50 years if the residual mean diameter following thinning was 12–20 cm. In the Llancahue forest, the first thinning rendered an average of 70–80 m of firewood (US $ 20 per meter), so that these were commercial thinnings (Donoso et al. 2014b). This may not occur in the Correntoso forest with smaller trees. The second thinning should render firewood in any case, but also some small sawlogs. A third and probably a fourth thinning would be likely needed to reduce densities to 300–500 trees per ha. A final shelterwood cut should be used to favor regeneration of this group of midtolerant tree species (maintain a tree cover that prevents regeneration of the pioneer Proteaceae species) and should be conducted to harvest large proportions of veneer timber.

A two-stratum management would require a mixed thinning method, with a reduced density of the upper canopy layer that would allow more light to penetrate to the second strata. In this case, the idea would that once the upper layer reaches the expected 35 cm in mean diameter, not all trees should be harvested following an even-aged silvicultural method, but some 50 trees per hectare should be left standing to continue providing some partial shade to the more shade-tolerant species. This would then be similar to a delayed shelterwood method (Nyland 2002). The final cut should then be conducted when trees in the second strata reach the expected final diameter. If final diameter for this stratum is 35 cm, most likely the trees in the upper stratum will have diameters close to 50 cm. This two-stratum management then would likely make a more efficient use of the site, with a mixture of species of different tolerances, growth rates, phenology, and likely rooting pattern species (requirements for mixed-species silviculture; Kelty et al. 1992). In addition, this management scheme would probably be more economically attractive, with greater volumes harvested in trees of greater value due to their larger diameters, but this has yet to be estimated. These analyses could recommend different threshold diameters, but schemes with trees providing timber for veneer may generate a larger profit (Navarro et al. 2010).

8.2.2.2 *Drimys winteri*-Dominated Secondary Forests

Secondary forests dominated by *D. winteri* have a catastrophic mode of regeneration (clearcuts, fires, abandoned prairies) and start as highly dense even-aged communities. They usually grow on gentle slopes and even flat terrains, at elevations below 400 m a.s.l, under oceanic influences that moderate temperatures. They grow throughout and ample region from north to south (600 km; 39–43°S) and east to west (100 km from the coast to the lower Andean slopes in Chile), which illustrates the ecological plasticity of the species. Across this geographic distribution, different levels of productivity can be found for secondary forests dominated by *D. winteri*, which coupled with diverse restrictions for silviculture determine the options for defining management objectives. Also different degrees of mixtures can be found in forest stands dominated by *D. winteri*, adding another consideration for defining the prospects of management of these forests.

The best forest sites are found with increasing latitude, and particularly in the coastal zone between 41° and 44°S, and the poorest in the extreme zones of the distribution of these forests between 38 and 39°S and between 43 and 44°S, where soil moisture is lower and temperature oscillations are higher (Navarro et al. 1997).

For those forests where the main production objective is high-quality timber, and the secondary objective is the provision of services, it is possible to propose either even- or uneven-aged silvicultural systems. The high-quality timber of several accompanying species of *D. winteri* in these mixed forests, such as *E. cordifolia*, *N. nitida*, *L. philippiana*, *S. conspicua*, and *P. nubigena*, provides these alternative silvicultural systems. One-stratum even-aged management could consider only *D. winteri* and *N. nitida*, which share the main canopy in these even-aged forests (Donoso et al. 2007), while two-stratum or uneven-aged management could include most of these species, although *L. philippiana* is the one that has shown the highest regeneration abundance under the dominant tree canopies of either unmanaged (Soto and Donoso 2006) or managed (Navarro et al. 2010).

For the current state of *D. winteri*-dominated secondary forests (pole size and small sawtimber size), for more productive sites, it is needed to apply thinnings as the most important silvicultural activity, due to the high mortality rates that unmanaged forest area is experiencing (Navarro et al. 1997). In this regard, the suggested management zone for these forests is between 30% and 45% relative densities and three to four thinnings to reach stands with mostly veneer and large sawlog timber. This would happen at an age of at least 80 years with a final number of 400–500 pro hectare for a final harvest with a mean diameter of 40 cm. Density control can be guided with size-density relationships (Donoso et al. 2007) or stand density diagrams (Navarro et al. 2011) developed for these forests.

8.2.3 Uneven-Aged Silviculture in Mature and Old-Growth Forests

Little experience exists in Chile in regard to uneven-aged silviculture. This is surprising considering that there are 4.8 million hectares of mixed old-growth forests between the Maule (36°S) and the Aysén (47°S) regions in Chile (www.sit.conaf.cl). These old-growth forests are in different states of conservation, but likely most accessible ones are partially or severely high-graded. Donoso (2002) studied the potential for uneven-aged silviculture in old-growth forests of the EFT and basically proposed the convenience to use this silvicultural approach in these forests considering the dominance of midtolerant and shade-tolerant species and the multilayered and multiaged structure of these forests. He proposed residual basal areas of 35–50 m^2 ha^{-1} and final basal areas of 55–50 m^2 ha^{-1} before a new entry to the stands (mature harvest diameter at 70–80 cm). Later he implemented selection cuttings with residual basal areas of 40 and 60 m^2 ha^{-1} with the hypothesis that the ones with lower residual densities would better favor the regeneration of *E. cordifolia*, one of the most valuable species in these forests. Schnabel et al. (2017) evaluated the early effects of these cuttings upon structure and composition of these forests and concluded that these cuttings maintained most of the attributes of old-growth forest range, but especially the height range, which were reduced in their higher limits mostly in the lower density cuttings. While regeneration has not been evaluated yet, it seems to be developing well for all most important species (e.g., *D. winteri*, *Podocarpus saligna*, *A. punctatum*, *L. philippiana*) but *E. cordifolia* suffers a lot of browsing from domestic cattle (personal observation PJ Donoso). These species have low diameter growth rates when unmanaged (from 1 to 4 mm $year^{-1}$), but it is expected that they should at least double their growth rates. If that was the case, Donoso and Pilquinao (2013) estimated that cutting cycles for these forests with residual densities of 40 m^2 ha^{-1}, final densities of 55 m^2 ha^{-1}, and mature harvest diameters of 70–80 cm should be of 14–15 years, instead of 5 years that the current law for "selective" harvesting allows in Chile.

8.3 "A Close-to-Nature" Management Concept for Second-Growth Mixed Nothofagus Forests in South-Central Chile

8.3.1 Distribution and Ecology

Among natural forests, second-growth mixed *Nothofagus* forests dominated by *N. obliqua*, *N. alpina*, and *N. dombeyi* of south-central Chile are important for timber production because of their high wood quality and their accessible location in the most productive sites of south-central Chile (Salas et al. 2016). The current distribution of these forests is mainly the result of natural succession after intensive harvesting or abandonment of agricultural land.

The first silvicultural regulation for second-growth *Nothofagus* forest management was introduced by the Chilean National Forest Corporation (CONAF) in 1993 and was based on minimum stocking requirements for thinning. In the following decades, several stocking diagrams were developed, following Gingrich (1967), to support thinning operations. They generally lead to a simplified forest structure (Gezan et al. 2007; Müller-Using et al. 2012). The present contribution is thought to be a complement to these numerical tools, proposing a "close-to-nature" silvicultural concept based on the actual knowledge of the natural dynamics of *Nothofagus* species.

South-central Chile is frequently object of catastrophic natural disturbances such as earthquakes, volcanism, and strong storms, among others. After the occurrence of a disturbance, ecological succession begins with the establishment of pioneer species (Veblen et al. 1980). In the absence of catastrophic disturbances, the natural succession tends toward very diverse forests composed of shade-tolerant species (Brun 1975; Burschel et al. 1976). The secondary forests described here may either be pure or mixed in various proportions of the deciduous *N. obliqua* and *N. alpina* and the evergreen *N. dombeyi*. Depending on the successional stage, other evergreen broadleaf species are generally present in these forest stands, including *Eucryphia cordifolia*, *Laurelia sempervirens*, *Laureliopsis philippiana*, *Persea lingue*, and *Aextoxicum punctatum* (Grosse and Quiroz 1999; Grosse et al. 2006; Elgueta 2013). As a component of old-growth evergreen rain forests, these species have been regarded as commercially valuable, but in the actual state of secondary forests, they rarely are considered as an object of silvicultural interest, because their lower growth rates in the initial states are under the dominant *Nothofagus* stratum.

Assessment of Area, Species, Composition, and Structural Parameters
To characterize the second-growth forests, in 2011 the Chilean Forest Research Institute (Instituto Forestal, INFOR) collected data based on a regional forest inventory design. The area included was the extension covered by mixed second-growth stands of *N. obliqua*, *N. alpina*, and *N. dombeyi* between 36° and 40°33′S (Bio Bio, Araucanía and Los Ríos Region), representing a total area of 989,960 ha. The forest inventory was based on a systematic sampling grid of 1 km by 1 km. This grid size considered the fragmentation of the resource in coastal areas and the Central Valley. Each node of the grid within the polygons defined as second-growth forests of *N. obliqua*, *N. alpina*, and *N. dombeyi* presented a potential sampling point. For the final sample, a random selection resulted in 200 sampling units. Each cluster contained three 500 m^2 circular plots (Müller-Using et al. 2012; Bahamondez and Thomson 2016).

Using the data gathered in the forest inventory, we generated estimates of mean tree density, mean basal area, gross and net volume, and quadratic mean diameter (QMD) (Table 8.2).

In addition to the general descriptors, the samples were classified according to their structure in order to identify the most frequent situations and to propose silvicultural models for them. For this purpose, the 200 samples of the inventory were analyzed. The main factor for this analysis was the composition of the species

Table 8.2 Mean tree density, basal area gross, and net volume and QMD in second-growth *Nothofagus*-dominated forest stands between 36° and 40°33′S, south-central Chile

Variables	Mean	Precision (%)
Tree density (N ha^{-1})	582	8.74
QMD (cm)	23	7.77
Basal area (m^2 ha^{-1})	24	7.77
Gross volume (m^3 ha^{-1})	212	8.18
Net volume (m^3 ha^{-1})	149	9.87

Table 8.3 Composition and structure of the sampled second-growth *Nothofagus*-dominated forests

Stand structure	Description	Frequency of total sample plots (%)
A. Second-growth *Nothofagus* with low or null participation of shade-tolerant species		
A.1 Second-growth *N. obliqua* and/or *N. alpina*	>90% *N. obliqua* and/or *N. alpine*	52
A.2 Second-growth *N. dombeyi*	>50% *N. dombeyi* with other *Nothofagus* and/or tolerant species	11
B. Second-growth *N. obliqua* and/or *N. alpina* with tolerant species in different developmental stages		
B.1 Dominant strata of *Nothofagus* and well-developed secondary strata of evergreen, shade-tolerant species	50–90% *N. obliqua* or *N. alpina* with shade-tolerants in the same third of the diameter range	14
B.2 Dominant strata of *Nothofagus* with participation of evergreen shade-tolerant species beginning to form secondary strata	>50% *N. obliqua* or *N. alpina* with shade-tolerant species in the third lower diameter range. At least 1000 individuals per hectare	12
Other mixtures	<30% *N. obliqua* or *N. alpina*, <50% *N. dombeyi* or *Nothofagus* but none of the other mixtures	11

and the relation between the state of succession of the (one or several) main and the secondary species. The classification obeyed the following rules: a stand was defined as deciduous *Nothofagus* forest with low or null evergreen species, when the basal area of *N. obliqua* and/or *N. alpina* was equal to or greater than 90% of the total basal area. Due to the very similar dynamics and wood properties, for this silvicultural proposal, we didn't differentiate between these two species, so stands included in this category may be monospecific or a mixture of both. In forest with more than the indicated participation of evergreen non-*Nothofagus* species, the diameter range of the sample plot was divided in three equal size classes, and the structure was defined based on whether shade-tolerant species shared the same diameter range as *Nothofagus* species or not. For the evergreen *N. dombeyi*, the applied criterion was another because of the different morphology of their crowns. Here we classified as *N. dombeyi*-dominated forest, when the basal area was equal to or greater than 50%. In case of a minor participation of *N. dombeyi* or less than 30% for *N. obliqua* and *N. alpine*, the plots were classified as other mixtures. The results of this classification process are shown in Table 8.3.

8.3.2 *From Forest Dynamics to Silviculture*

Uebelhör (1984) developed a successional model for *Nothofagus*-dominated forests in south-central Chile. He has based this on the hypothesis that the development of these forests in the Andean foothills in the province of Valdivia is a very slow process due to the frequency of disturbances, which is why the final stage dominated by shade-tolerant species is not very common. Windthrow, where individual trees, groups of trees, or whole areas fall, is considered the most frequent cause for the regeneration of shade midtolerant (hereafter "midtolerant") and shade-intolerant (hereafter "intolerant") pioneer species. Although Uebelhör (1984) considers that Veblen and Ashton (1978) and Veblen et al. (1989) overestimate the frequency and scope of geological disturbances such as earthquakes and volcanic eruptions, he vastly agrees with them and other authors on the dynamics of *Nothofagus* forests (Donoso 1993).

Although the model dynamics for *Nothofagus*-dominated forests proposed from Uebelhör (1984) (Fig. 8.4) is a simplification of a complex successional process, we consider that it is adequate and useful as a tool for close-to-nature management of second-growth mixed stands. It integrates the main theories on natural dynamics for these forests and indicates the consecutive stages of succession from the colonization of open areas to a potential final stage, also considering that disturbances might occur, causing a regression to a preceding stage. It can be observed that from the early developmental stages until the final stage, the participation of evergreen species (shade-tolerant and midtolerant) increases. Conversely, the presence of shade-intolerant or midtolerant *Nothofagus* species decreases.

Because of its lineal flow chart design, it is easy to locate the situation of a specific forest, turning it into a very useful management tool (Cabello 2005; Donoso and Lara 1998; Grosse 2009). As a near-to-nature concept, it should maintain biodiversity, genetic variability, and productive potential (Pro Silva 2012). Our proposal intends to represent the different successional stages. Trying to combine high growth rates and good quality timber production with increasing biodiversity, through the presence of shade-tolerant and midtolerant species, the accent is placed on mixed stands with a high participation of *N. obliqua*, *N. dombeyi*, and/or *N. alpina*, representing phase 4 in Uebelhör's dynamic model (Figs. 8.4 and 8.5). This combination also diminishes the risk of plagues and diseases due to a more complex vertical structure of the forest acting as a natural barrier to flying insect, such as the coleoptera *Holopterus chilensis*, which can seriously affect the most valuable trees (Cabrera 1997; Baldini and Pancel 2002). Furthermore, in comparison with pure *Nothofagus* stands, mixed stands prevent the establishment and expansion of bamboo (*Chusquea* spp.), which in turn hinders further regeneration (Veblen and Donoso 1987). It is important to mention that these indirect advantages are not the only reasons to include the shade-tolerant and midtolerant species, as they also provide high-quality wood.

Considering forest dynamics and the current structure of Chilean forests, we propose three silvicultural management models, one for each structural situation identified in the inventory results. These are (A) an even-aged management model for *Nothofagus* stands without evergreen species, (B1) management in two strata for mixed stands with high participation of *Nothofagus* species, and (B2) a uneven-aged continuous cover management for forests with low participation of *Nothofagus*

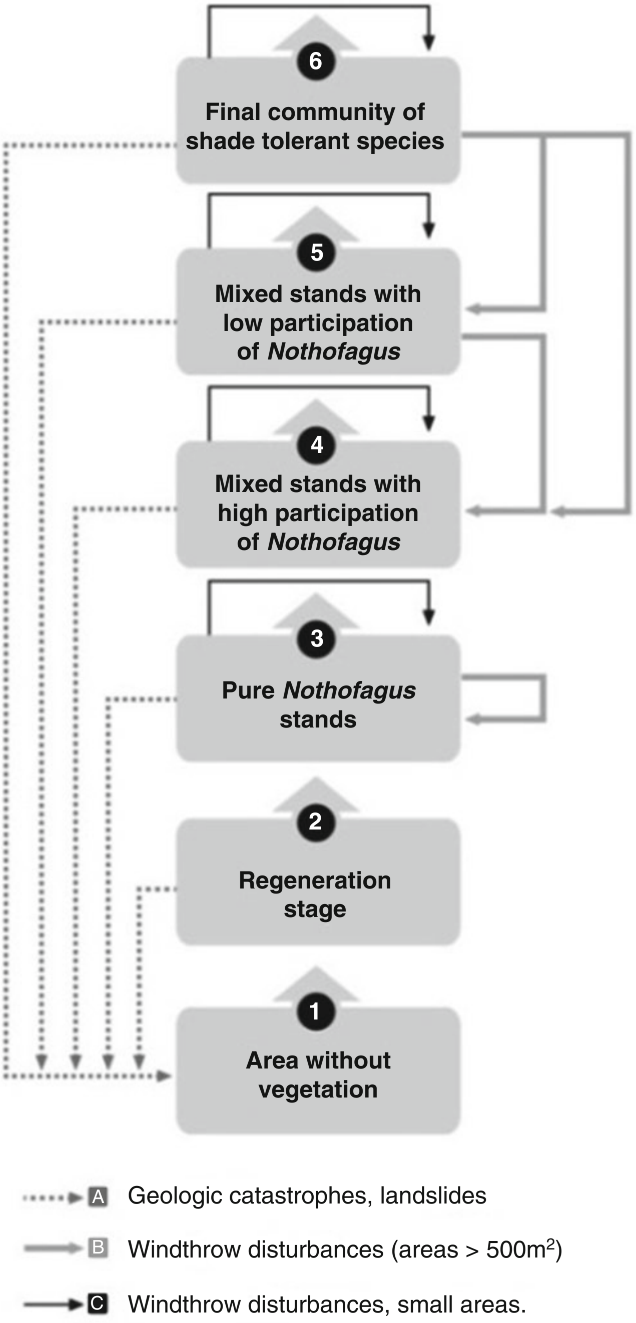

Fig. 8.4 Successional pattern of *Nothofagus* forests in south-central Chile (Uebelhör 1984)

Fig. 8.5 *Nothofagus obliqua* stand with temperate evergreen species in the second strata

species, based on a group selection system. For each situation, we defined recommendations concerning the main silvicultural objectives, reference densities for thinnings, and regeneration methods. This information is described for three case studies below and summarized in Table 8.4.

8.3.3 Case Studies

In order to illustrate this management concept, we selected three examples of characteristic stands, one for each structure type, and explain the silvicultural treatment for each of them (Figs. 8.6, 8.7, and 8.8).

The first stand diagram (Fig. 8.6) shows a nearly pure *N. obliqua* stand. The successional stage corresponds to stage 3 of Uebelhör's model, where we often find a mixture of *N. obliqua* and *N. alpina*. The management objective is sawtimber under a relatively simple management model, as there is only one tree stratum. The rotation age, reaching diameters of 45 cm, extends to 60–80 years, where two or three thinnings will be necessary to maintain the basal area at 30% of maximum tree density. In this range, the increment in value is highest (Lara et al. 2000; Steuer 2008). At final harvest the standing volume in such a management model may be 404 m^3 ha^{-1} with an average annual growth of 10.1 m^3 ha^{-1} (Donoso et al. 1993b). A transition toward mixed forests with dominant *Nothofagus* (successional stage 4) can be planned for the next rotation, incorporating shade-tolerant species in the natural regeneration process.

Table 8.4 Silvicultural management concept for *Nothofagus*-dominated second-growth forests in south-central Chile

Structure type	Future structure according to the successional stages from Uebelhör (1984)	Proposed management system	Objectives and management recommendations
A. Second-growth *Nothofagus* with low or null participation of shade-tolerant species	Stage 3, only *Nothofagus*	Even-aged method	*Nothofagus* timber production. Reference basal areas 30% relative density for *N. obliqua*, *N. alpina*, and 40% for *N. dombeyi* according the density management diagram developed by the Chilean Forest Research Institute (Müller-Using et al. 2012). Regeneration can be established by small clear-cuts of at least 0.1 ha (Grosse et al. 1996; Reyes et al. 2014). Rotation length between 60 and 80 years
B. Second-growth *N. obliqua* and/or *N. alpina* with tolerant species in different development stages	Stage 4–5, mixed stands with participation of *Nothofagus*	1. Two-aged method	Timber production from *Nothofagus* with high heartwood proportion and other valuable shade-tolerant evergreen species. Relative density for management about 35%. Long rotation system, 125 years. Regeneration in gaps, regeneration of *Nothofagus* species must be established artificially
	Stage 4 mixed stands with low participation of *Nothofagus*	2. Uneven-aged method	Saw-wood production from *Nothofagus* with high heartwood proportion and other valuable shade-tolerant evergreen species. The concept of relative density does not apply for this uneven-aged continuous cover management system. Regeneration occurs in small gaps

In mixed *Nothofagus* forests with evergreen species, the developmental stage of the evergreen stratum can be evaluated according to its advance in relation to the *Nothofagus* stratum. If there is a dominant *Nothofagus* stratum with small tree

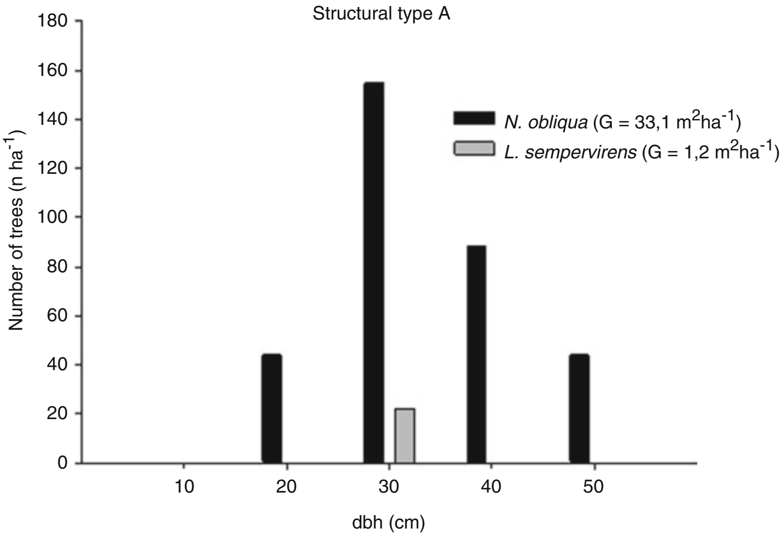

Fig. 8.6 Diameter structure for a nearly pure *Nothofagus* stand (type A). (Data from the Chilean National Forest Inventory)

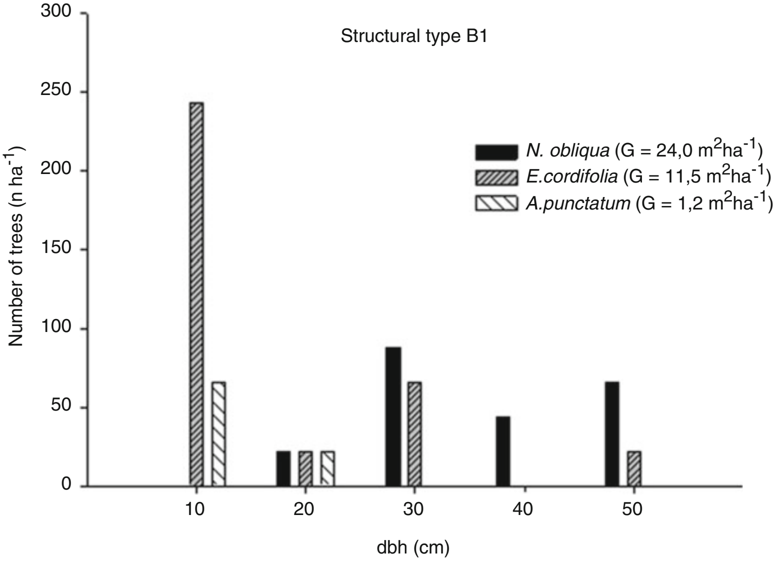

Fig. 8.7 Diameter structure for a mixed stand with a dominant stratum of *Nothofagus* and second stratum of shade-tolerant evergreen species (type B1). (Data from the Chilean National Forest Inventory)

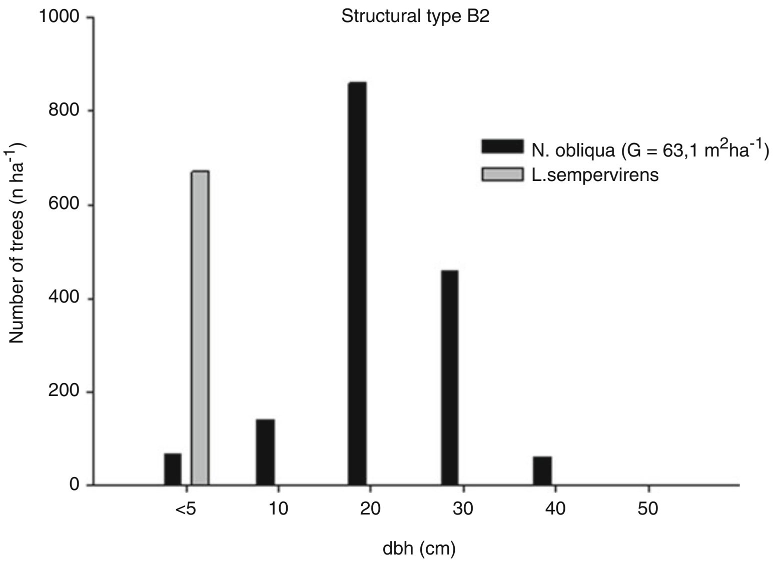

Fig. 8.8 Diameter structure for a mixed stand with a dominant stratum of *Nothofagus* and a very young second stratum of evergreen and shade-tolerant species (type B2). (Data from the Chile-an National Forest Inventory)

diameters and a complete second stratum of evergreen species, filling the spaces between the stems of the first stratum (type B1, Fig. 8.7), a two-stratum management model is recommended. This model is orientated toward "Mixed forest with high participation of *Nothofagus*" (Uebelhör's successional stage 4).

In this model production focuses on a diversity of products, such as timber with high proportion of heartwood of *Nothofagus* species and younger softwood timber of other species. In this management system, two rotations overlap: one is the dominant layer of *Nothofagus*, in which 75% of trees are harvested when they reach a dbh of 45 cm, and the other is shade-tolerant species with the 25% of now large remnant *Nothofagus* stems with a very high valuable heartwood proportion. In the following rotations, this model continues as a system of alternating harvests between a stratum of *Nothofagus* and the stratum of evergreen more shade-tolerant species. In Uebelhör's diagram, this model lies between stages 3 and 5. Regeneration of *Nothofagus* species must be established artificially as only few *Nothofagus* parent trees will remain. This management model considers a higher-density pure *Nothofagus* forests. Average annual increments are estimated in 8.7 m^3 for *Nothofagus* stratum and 5.3 m^3 for evergreen species (data from National Forest Inventory). Because of the additive growth effect (Donoso and Lusk 2007) of the two strata, we recommend to maintain it about 35% of maximum tree density. The expected production goal of this model is approximately 807 $m^3\ ha^{-1}$ (Rojas et al. 2010).

In the third situation, evergreen species are beginning to occupy the middle stratum under a dominant *Nothofagus* stratum (type B2). This situation is

Table 8.5 Seedling and sapling density in understory strata and species shade-tolerance

Species	Seedlings (n ha^{-1})	Saplings (n ha^{-1})	Shade-tolerance
E. cordifolia	117	204	Midtolerant
L. sempervirens	468	331	Midtolerant
P. lingue	796	64	Tolerant
D. winteri	70	140	Midtolerant
A. luma	70	267	Tolerant
L. hirsuta	70	127	Intolerant
E. coccineum	468	140	Intolerant
Total	2059	1273	

represented in Fig. 8.8, and complete regeneration data for this stand is given in Table 8.5. For this situation, we included the regeneration data because it is relevant for choosing the adequate management model. As we show in Table 8.5, it is characterized by the succession toward a mixed forest with low participation of *Nothofagus* species.

In this third situation, more time is required to integrate shade-tolerant species into the management, and their presence in the superior strata is a gradual and more individual process. In this condition, it is recommended to pass from even-aged to uneven-aged management. As in the case mentioned before, these stands are in the successional stage: "mixed forests with abundant *Nothofagus*" (Uebelhör's stage 4). The difference with the previous model is the change toward a permanent production system with evergreen species. Gradually the transition from stage 4 to stage 6 occurs. Data from Donoso and Pilquinao (2013) show for uneven-aged evergreen forests without management a volume range between 415 and 549 m^3 ha^{-1} and increments of 2.4 and 3.0 m^3 $year^{-1}$. This would be significantly higher under management.

8.3.4 Conclusions

Until now, the silvicultural treatments of *Nothofagus* second-growth forests in south-central Chile has been focused mainly on optimizing thinning operations, where the first successional stage after disturbance, with pure *Nothofagus* pioneer species, has been the object. Analyzing the data provided by a regional inventory of this forest resource, we found three different types of tree species mixtures, which can be associated with distinct successional stages of second-growth forests. Doing so, we are able to leave behind a focus that only considers a single option for stand intervention. This perspective provides the opportunity for a more holistic management which defines the prescription on the basis of the natural trend of stand development. This concept conceives longer rotation times with greater development of species diversity, leading to an increasing variety of wood products and environmental benefits, such as higher resilience, more carbon stocking, and greater soil protection.

8.4 Subantarctic Forest of *Nothofagus alpina*, *Nothofagus obliqua*, and *Nothofagus dombeyi* from Argentina: Structure, Dynamics, and Silviculture

8.4.1 Distribution and Ecology

In Argentina, along the eastern foothills of the Andes between 39°29′–40°22′S and 71°15′–71°40′W, and up to 1000 m a.s.l., in areas with annual precipitation of 1000–2000 mm and deep and drained volcanic soils, mixed subantarctic *Nothofagus* forests occur. The deciduous *N. alpina* and *N. obliqua* and the evergreen *N. dombeyi* are the dominated tree species and cover 44,000 ha (CIEFAP-MAyDS 2016). Here, hybridization between *N. alpina* and *N. obliqua* occurs naturally (Gallo et al. 2000). *Nothofagus* are decline monoecious trees showing wind pollination and anemocory, limited seed dispersal, and a 4-year reproductive cycle for the formation of a cohort (Riveros et al. 1995). They exhibit masting, annual seed production estimated in 4900 seeds m^{-2}, and a transitory soil seed bank (Dezzotti et al. 2016). Seeds of *N. dombeyi* are intrinsically lighter (Burschel et al. 1976; Dezzotti et al. 2016) (Table 8.1). Recently fallen seeds are frequently pre- and post-dispersal predated and vain probably due to self-fertilization, and germination increases during most fertile periods (Burschel et al. 1976; Donoso 1993; Donoso et al. 1993a; Bustamante 1996; Figueroa et al. 2004; Dezzotti et al. 2016).

Nothofagus shows interspecific divergences judging from ecological and physiological evidence (Table 8.1). Niche differentiation among species is mainly related to light and manifests early, and it would explain the variability in stand structure within this mixed forest type (Müller-Using and Schlegel 1981; Weinberger and Ramírez 2001; Donoso et al. 2013). *Nothofagus dombeyi* is the most light-demanding, whereas *N. alpina* is the most shade-tolerant tree. In natural forest, *N. alpina* tend to present an asymmetric left-handed size distribution, due to a greater abundance of smaller individuals under the canopy (Donoso et al. 2014a). After selective cuttings, the original balanced composition tends not to be maintained because of the lower competitive ability of *N. alpina* regeneration after the increased radiation of the forest floor (Dezzotti et al. 2004). In plantation, *N. dombeyi* exhibited a better response to larger whereas *N. alpina* to smaller gaps (Grosse 1988; Donoso et al. 2013). The persistence of *N. alpina* in intermediate shade was related to low respiration and light compensation point (Read and Hill 1985) (Table 8.6). In addition, seed weight tended to correlate with tree temperament: heavier seeds exhibit less anemocory, and plants are adapted to shaded habitats under canopy (*N. alpina*), while lighter ones are dispersed by wind at greater distance, and plants develop in sunny areas of gaps (*N. dombeyi*).

Table 8.6 Characteristics of *N. alpina*, *N. obliqua*, and *N. dombeyi*

Characteristic	*N. alpina*	*N. obliqua*	*N. dombeyi*
Subgenus[a]	*Lophozonia*	*Lophozonia*	*Nothofagus*
Range (S latitude)[b]	36°30′–40°30′	32°50′–41°30′	36°30′–47°00′
Leaf type, texture, size (cm^2)[c, d]	de, ca, 6.6	de, ca, 4.7	pe, co, 1.8
Specific leaf area ($cm^2\ g^{-1}$)[e, f]	338–417, 418	228–442, 366	137–316
Foliar area ($cm^2\ ind^{-1}$)[e, h]	100.6, 113.5	78.9, 135.4	64.1, 39.1
Relative foliar area ($cm^2\ g^{-1}$)[e, f]	79–98	54–104	58–134
Seed weight (mg)[h, i, j]	3.8–13.3	6.2–24.4	0.6–4.4
Seed production (seed ind^{-1} $year^{-1}$, seed ha^{-1} $year^{-1}$)[i]	26,900–140	244,700–540	765,000–4220
Sapling stem length/root length[g]	1.2	1.5	1.8
Anemocory[j]	Lower	Intermediate	Higher
Vegetative reproduction	Yes	Yes	No
Chlorophyll (10^{-5} g cm^{-1})[e]	2.7	3.6	4.9
Light compensation point (μmol m^{-1} s^{-1})[e]	9	16	17
Photosynthetic efficiency (μmol m^{-1} s^{-1})[e]	0.027	0.019	0.018
Net photosynthesis max. (μmol m^{-1} s^{-1})[e]	6.0	6.7	6.6
R_{dark} (μmol m^{-1} s^{-1})[d]	0.6	0.9	1.1
Light intensity for germination (min., %)[e]	3.1	2.2	3.9
Cyttaria[j]	*Cs*	*Cs*, *Cb*	*Ch*, *Cj*
Heterobathmia[k]	Yes	Yes	No

[a] Hill and Jordan (1993)

[b] Veblen et al. (1996)

[c] *de* deciduous, *pe* perennial, *ca* cartaceous, *co* coriaceous (Romero 1980)

[d] Müller-Using and Schlegel (1981)

[e] Read and Hill (1985)

[f] Dezzotti (2008)

[g] Donoso and Cabello (1978) and Marchelli and Gallo (1999)

[h] Dezzotti et al. (2016)

[i] Burschel et al. (1976) and Veblen et al. (1996)

[j] Genus of gall-forming parasitic fungi exclusive of *Nothofagus*. *Cs C. spinosae*, *Cb C. berteroi*, *Ch C. hariotti*, *Cj C. johowii* (Humphries et al. 1986)

[k] Genus of Lepidoptera whose larvae are miners of *Nothofagus* (Kristensen and Nielsen 1983)

The dynamics of these subantarctic forests is influenced by the light-demanding, opportunistic character of *Nothofagus* species and their capacity to endure harsher conditions than neighboring tree species, the disturbance regime, and the physical environment that abruptly changes following an E-W direction. In the eastern flanks of the Andes in Argentina, *Nothofagus* rapidly colonizes open sites forming even-aged populations following the synchronous elimination of previous vegetation, caused by the periodical occurrence of large-scale disturbances.

These allogenic impacts are mainly natural and anthropogenic fires. In this initiation stage of succession, *Nothofagus* follows a “catastrophic regeneration mode.” During stem exclusion stage, self-thinning drastically reduces density and

Table 8.7 Structure of three unmanaged stands of *N. alpina* (*Na*), *N. obliqua* (*No*), and *N. dombeyi* (*Nd*) in understory reinitiation (*) and old-growth stages (**) from the Lanín Reserve

Site	Variable	Species						Total / *Mean*
		Na	%	*No*	%	*Nd*	%	
Quilanlahue $^{(**)}$	*D*	–	–	80	42	110	58	190
40°08′ 60″S	*BA*	–	–	13.9	28	35.0	72	48.9
71°28′ 00″W	*V*	–	–	173.8	16	926.1	84	1099.9
750 m a.s.l.	dbh_c	–	–	47.0	–	63.7	–	55.4
	$h_{\max}$	–	–	40.7	–	38.0	–	39.4
	Cc	–		18.1	22	52.8	66	70.9
Yuco $^{(*)}$	*D*	40	9	380	83	40	9	460
40°08′ 49″S	*BA*	5	9	42.8	73	10.5	18	58.3
71°30′ 19″W	*V*	57.9	7	450.5	57	283.4	36	791.8
844 m a.s.l.	dbh_c	39.8	–	37.8	–	57.8	–	45.1
	$h_{\max}$	34.2	–	34.7	–	37.0	–	35.3
	Cc	11.1	13	68.1	78	8.3	9	87.5
Chachín $^{(**)}$	*D*	30	30	–	–	70	70	100
40°09′ 50″S	*BA*	19.5	33	–	–	39.2	67	58.7
71°39′ 00″W	*V*	271.1	20	–	–	1071.0	80	1342.1
700 m a.s.l.	dbh_c	91.0	–	–	–	84.4	–	87.7
	$h_{\max}$	35.8	–	–	–	45.0	–	40.4
	Cc	18.1	23	–	–	54.2	70	72.3

D density (ind ha^{-1}), *BA* basal area (m^2 ha^{-1}), *V* volume (m^3 ha^{-1}), dbh_c mean quadratic diameter at breast height (cm), $h_{\max}$ maximum tree height (m), *Cc* crown cover (%) (Dezzotti et al. 2016)

increases biomass of trees. In the absence of large-scale disturbances, understory replenishment may start with seedlings in a "gap-phase regeneration mode," when small- (<500 m^2) to medium-sized light gaps (500–2500 m^2) are opened up by the fall of senescent, old-growth individuals after 150–200 years (Veblen et al. 1996) during the understory reinitiation stage.

Although *Nothofagus* is formed by gap-dependant trees, in large openings mortality of immature individuals can be high due to the extreme temperatures of a climate with marked seasonality (Dezzotti et al. 2004; Donoso et al. 2013). As a result of the absence of shade-tolerant trees, neither successional replacement of *Nothofagus* nor change in species composition is likely to occur. In the absence of coarse disturbances, small-scale ones produce environmental heterogeneity that promotes a shifting forest mosaic during the old-growth stage. In this region, mixed *Nothofagus* forests are mainly in the understory reinitiation and old-growth stages, although there are also fewer in the initiation and stem exclusion stages. Old-growth stands are single-cohort with unimodal size frequency distributions, with 40–70 m^2 ha^{-1} basal area and 900–1400 m^3 ha^{-1} volume, and with individuals of >300 years of age, >100 cm dbh, and 30–40 m height (Table 8.7).

Conversely, in the nonseasonal and floristically more diverse areas of the Valdivian district, in coastal and mountainous areas west to the Andes in Chile, *Nothofagus* tends to be successionally replaced by shade-tolerant, broadleaved, and conifer trees during advanced stages of forest development. However, the periodic occurrence of large-scale perturbations interrupts any directional change in community composition and maintains the *Nothofagus*-dominated forests (Veblen et al. 1996).

Chusquea culeou (E. Desv. Poaceae) is the most frequent and abundant component in the understory and clearings of different size and origin in this mixed forest (Veblen et al. 1996). Colonization and early development of *Nothofagus* are impaired by its massive proliferation and by the thickness of the litter that develops beneath the main canopy that constitutes an unsuitable seedbed (Burschel et al. 1976). It shows a vegetative phase of between 14 and 50 years, after which it flowers and dies in a gregarious and synchronous mode (Lusk 2001). This process dramatically changed rapidly light, temperature, soil organic matter, nutrient cycling, and granivorous demography (Giordano et al. 2009; Austin and Marchesini 2012). After flowering and massive senescence of *C. culeou*, *Nothofagus* would occupy sites through seed, regrowth, or advance regeneration. However, its ability to compete with *C. culeou* is reduced because of a lower seed production and seedling emergence, growth, and survival (Dezzotti et al. 2016).

8.4.2 Stand Growth and Productivity

Dominant height-age curves for *Nothofagus* species were available as productivity and quality site indicators, which were adjusted using the model of von Bertalanffy-Richards. According to this model, the three *Nothofagus* species exhibited an anamorphic pattern of growth of dominant height for the different classes of site quality. *Nothofagus dombeyi* exhibits the largest growth in dominant height; however, the three species attains 40 m at 100–110 years in the best quality sites (Attis Beltrán et al. 2018) (Fig. 8.9). Diameter growth models indicate differences in tree

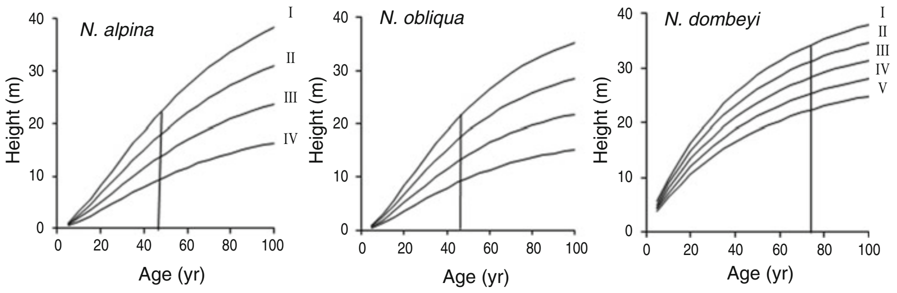

Fig. 8.9 Dominant height-age curves of Nothofagus within the Lanín Reserve based on site index at a respective reference age (ra) at dbh. For *N. alpina* and *N. obliqua*, ra = 45 year and site class *I*, 19; *II*, 19–15; *III*, 14.9–11; and *IV*, <11 m. For *N. dombeyi*, ra = 75 year, *I*, >33; *II*, 33–30; *III*, 29.9–27; *IV*, 26.9–24; and *V*, <24 m (Attis Beltrán et al. 2018)

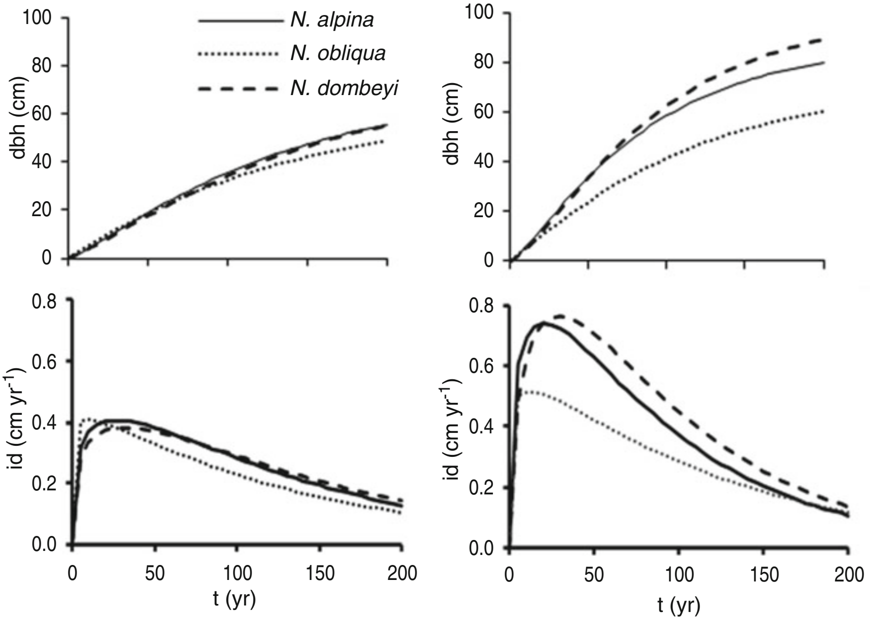

Fig. 8.10 Diameter at breast height (dbh) and current diameter increment (id) along time for *N. alpina*, *N. obliqua*, and *N. dombeyi* of the intermediate (left) and dominant and codominant strata (right) based on growth models (Attis Beltrán et al. 2018)

performance related to species and social strata (sensu Smith et al. 1996). For the dominant, codominant, and intermediate stratum, *N. dombeyi* shows the largest values of maximum asymptotic diameter, and *N. obliqua* exhibits the smallest. For the dominant and codominant stratum, *N. dombeyi* and *N. alpina* exhibit the largest absolute and maximum diameter growth, whereas for the intermediate stratum, the three species show a similar increment (Attis Beltrán et al. 2018) (Fig. 8.10).

8.4.3 Forest Management and Silviculture

In the Lanín National Park (39°7′–40°40′S, 71°42′–71°12′W), current legislation permits forest management as a strategic conservation policy, but strictly in zones categorized as reserve (195,010 ha, 47.3% of the area). Here, selective cuttings started at the beginning of the twentieth century and attained the largest extension and intensity during 1940–1960. This earlier activity was characterized by lack of planning, diffuse silvicultural prescriptions, weak governmental control, and short period licences. Felling was particularly directed to *N. alpina* and *N. obliqua* trees of commercial size. At present, the low proportion of large trees of both species in mixed stands and the numerous unmanaged stands dominated by *N. dombeyi*

Table 8.8 Prescribed remaining cover of shelterwood method in relation to cutting types and development stages applied to *Nothofagus* stands from the Lanín Reserve

Stages	Cutting type	Stage	Remaining cover	
			Crown (%)	Basal area (m^2 ha)
Regeneration	Preparatory	3, 4	70–80	30–35
	Establishment		40–50	25–30
	Secondary		30–40	15–25
	Removal		15–20	10–15
Conduction	Thinning	1, 2	80–90	15–30

1, stand initiation; 2, stem exclusion; 3, understory reinitiation; 4, old-growth

evidence this practice. However, the natural and anthropogenic fires that have occurred during the late nineteenth century also determine population structures (Veblen et al. 2003).

Sustainable management started in the late 1980s, and at present, there are about 1000 ha destined to obtain wood and firewood from trees and bamboo canes from *C. culeou*. Management units are located in Chachín, Nonthué, Yuco, and Quilanlahue, at 700–1050 m a.s.l. Considering species temperament, stand dynamics, and dominant mature structures, silviculture is carried out largely by the shelterwood system, which promotes establishment and growth of natural regeneration (Smith et al. 1996). The removal of the old stand is made in a series of cuttings that extends over a relatively short period of the rotation, usually one-fifth of the cutting period estimated in around 100 years, by means of which the establishment of one cohort of advance regeneration is encouraged (Table 8.8). Dominant, healthy, well-formed, and stable older trees, with the potential of further grow, are retained for variable periods. This is carried out to preserve a source of seeds until immature plants are established and help these plants to keep partly shaded and protected against freezing in winter and desiccation in summer. In addition, these trees are reserved for soil and drainage protection and aesthetic purposes. Reserved trees exhibit superior characteristics that in future interventions provide timber of greater relative value.

Standing, dead or dying, and fallen trees are kept in the forest site to preserve the structural complexity and promote the maintenance of the biological and functional diversity. Because a source of seeds is retained, this system allows implementing cuttings and then awaiting a good seed period.

Preparatory cuttings are implemented to strengthen the vigor of trees destined to be left in subsequent stages. Establishment cuttings should be implemented 20–30 years after preparatory cutting, with the aim to open up enough vacant growing space in a single operation to allow establishment of a new cohort under the protection of remaining adult trees (Table 8.8, Figs. 8.11, 8.12, and 8.13). This treatment involves the largest area within forest management plans. After 2–3 years of this last intervention, secondary cuttings are carried out in order to homogenize the spatial distribution of open areas for regeneration. Establishment cuttings are applied to gradually uncovering the new crop and making the best use of the

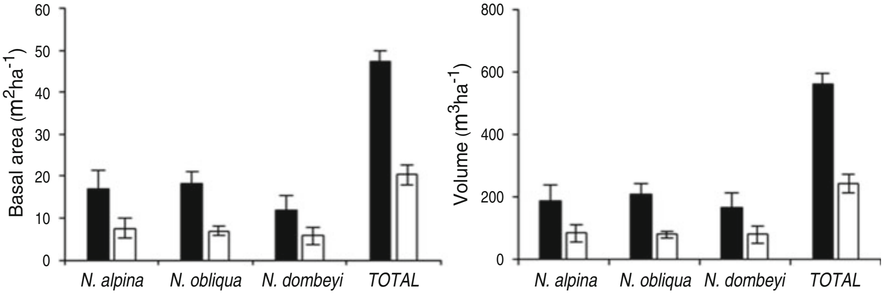

Fig. 8.11 Pre- (black bar) and harvest (white bar) basal area (left) and volume (right) for *N. alpina*, *N. obliqua*, and *N. dombeyi* in Yuco after preparatory and establishment cuttings. Vertical bars indicate the standard error of the mean ($n = 19$) (González Peñalba et al. 2016)

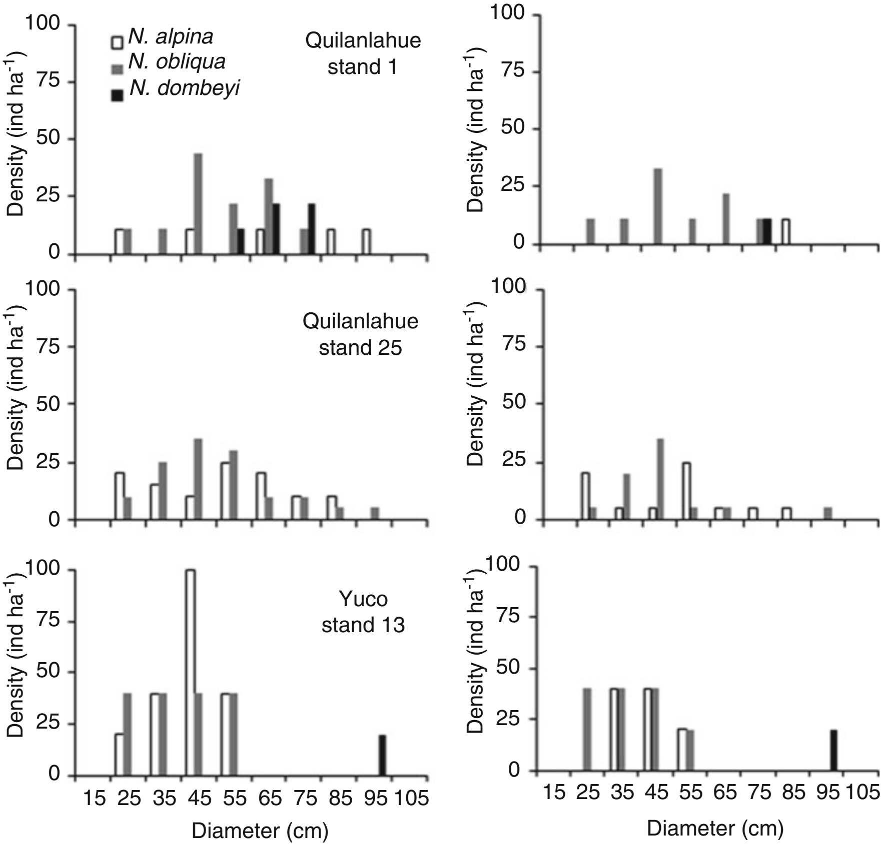

Fig. 8.12 Diameter at breast height frequency distribution of *N. alpina*, *N. obliqua*, and *N. dombeyi* before (left) and after (right) establishment cuttings in three stands within the Lanín Reserve (González Peñalba et al. 2016)

Fig. 8.13 Old-growth stands of *N. alpina*, *N. obliqua*, and *N. dombeyi* in Yuco showing adult and juvenile trees after 5 (left) and 15 years (right) of establishment cuttings

potential of remaining old trees to increase in value. Removal cuttings represent the last intervention of the regeneration period. However, this stage was not applied yet given that this period, estimated to be 25–30 years and involving a density of 2500 saplings ha^{-1} of height ≥ 2 m, was not fully attained. Rotation is estimated in 120–140 years; however, this age could be reduced to less than 100 years during future cohort management, based on research made in other regions (Lara et al. 1998). Conduction treatments as thinning are only carried out at experimental level, given the shortage of stands overpassing the initiation and stem exclusion stages (see *Thinning*).

8.4.3.1 Monitoring

Since 1988, continuous monitoring of management is made in circular and rectangular permanent sampling plots of 500–2700 m^2 each, located between 71°38′–71°26′W and 40°07′–40°10′S (González Peñalba et al. 2016). In these plots, composition, abundance, size, and growth of adult trees and natural regeneration and abundance of *N. obliqua* and *N. alpina* stump sprouts are evaluated every 5 years. The monitoring system consists of (i) 22 plots in stands under understory reinitiation and old-growth and subjected to establishment cuts, in which there were also installed subplots for evaluation of regeneration, and (ii) 8 plots in stands under initiation, in which part of them were subjected to crown thinning of the upper canopy, in order to release reserved trees from competition for future harvesting. In the lower stratum, small trees are not felled because they do not affect large trees and favor bole formation without lateral branches. The rest of the plots is unthinned and acts as control.

8.4.3.2 Growth and Production After Cutting

Considering silvicultural prescriptions (Table 8.3), in particular in the Yuco management area, 20.3 m^2 ha^{-1} of basal area (42.9% of pre-harvest) and 242.2 m^3 ha^{-1}

of volume (43.1%) were extracted. The contribution of each species in volume was 34.5% for *N. alpina*, 32.8% for *N. obliqua*, and 32.7% for *N. dombeyi* (Fig. 8.13). Within all management areas, after 10 years of cuttings, remnant trees exhibited a current diameter growth of 0.35 cm year^{-1} (SE = 0.04) and volume growth of 7.4 m^3 ha^{-1} year^{-1} (SE = 0.78), equivalent to 1.6% year^{-1} (SE = 0.12, $n = 6$) (González Peñalba et al. 2016).

8.4.3.3 Stump Sprouts

Although the main objective of shelterwood is to promote natural regeneration from seed, *N. obliqua* and *N. alpina* present vegetative reproduction too. In stands under shelterwood cut, the amount and conservation status of *N. obliqua* and *N. alpina* sprouts were recorded after 5 and 10 years of tree cutting. High proportion of stumps with live but poorly preserved sprouts, probably given progressive loss of vigor and mortality due to competition, would indicate a mean of four shoot stump after 15–25 years. Extensive sprout management should be applied to reach this value and anticipate the process of natural mortality. The size and growth of the dominant stumps (5.3 cm dbh, 5.9 m height) achieved height growth of 0.36 m year^{-1}.

8.4.3.4 Natural Regeneration

Before silvicultural intervention, mature stands have null or very low abundance of advance regeneration given the light-demanding temperament of all tree species and the large canopy cover that normally exceeds 80%. Shortly after establishment cuttings, colonization of a new tree cohort starts; however, at a given moment, age of the regeneration phase is variable because of the occurrence of 2–3 years of good seed production. Regeneration height of 2 m is reached after 10–15 years. In the Lanín Reserve, natural regeneration is a process in progress given that establishment cuttings were carried out less than 25 years ago. Current mean density of seedling (height <2 m) and saplings ($\geq$2 m) was estimated in 4963 and 5735 ind. ha^{-1}, respectively. The response of *Nothofagus* to felling was highly positive taking into account abundance, conservation status, and growth of tree recruitment, whose values largely exceeded prescriptions. However, domestic cattle must be excluded, and the thick litter layer of *C. culeou* should be weakened in regeneration areas (González Peñalba et al. 2016). The genetic effect of management on these young plants was evaluated, comparing species composition between upper and lower canopy and microsatellite markers. After 20 years of establishment cuttings, the original balanced composition of the adult component was not maintained in the regeneration; contrarily, no impact was detected in the gene pool at species level (Sola et al. 2016). However, monitoring is carried out continuously to record eventual changes on composition and structure of tree population related to species temperament, physical setting, and silviculture, in the context of adaptive management.

8.4.3.5 Thinning

The response to commercial crown thinning was only experimentally evaluated in stands overpassing the initiation stage, with mean tree ages between 43 and 57 years. This conduction treatment reduced the mean quadratic diameter by 7.7% and stand volume by 31.5%. After 10–15 years, dominant and codominant trees for the thinned stand exhibited diameter growth equal to 0.42 cm year^{-1} and current volume growth equal to 13.0 m^3 ha^{-1} year^{-1}, while for the untreated stand, values were 0.25 cm year^{-1} and 6.7 m^3 ha^{-1} year^{-1}, respectively. This preliminary trail showed that thinning implementation is recommended because it allows a significant increase in productivity and decrease in rotation age and is easy to apply as long as the individuals for releasing are clearly identified, provide poles and firewood with economic value, and can be implemented even if it is not the optimal moment. It is also recommended a precommercial thinning when stands attain 20–30 years.

8.5 *Nothofagus dombeyi-Austrocedrus chilensis* Forests

8.5.1 Distribution

Mixed forests of *Nothofagus dombeyi* and *Austrocedrus chilensis* are located east of the Andes, between 40 and 43°S, and occupy 32,800 ha (CIEFAP-MAyDS 2016) (Figs. 8.1 and 8.14). While *A. chilensis* grows on mesic and xeric sites, *N. dombeyi* only grows on mesic sites, with precipitation over 900 mm year^{-1}. Besides, where the precipitation is more than 1000 mm year^{-1}, there are woodlands and other forests that, naturally or through management, could be converted into mixed *N. dombeyi-A. chilensis* forests (Veblen and Lorenz 1987; Dezzotti 1996; Veblen et al. 2003).

These are:

Fig. 8.14 Landscape from *N. dombeyi-A. chilensis* forests with dead trees due *mal del ciprés* disease (left) and stand structure of them with regeneration of both species (right). (Photographs H. Gonda and M. Caselli, respectively)

(i) Pure *N. dombeyi* or *A. chilensis* with few individuals of the other species, covering 21,500 ha (CIEFAP-MAyDS 2016).

(ii) Post-fire mixed woodlands of *N. antarctica*, *Lomatia hirsuta*, *Schinus patagonicus*, and *Maytenus boaria*, which are seral stages toward high pure or mixed *N. dombeyi* or *A. chilensis* forests (Kitzberger 2012; Rusch et al. 2016). They extended northern from 43°S and occupy 52,000 ha (CIEFAP-MAyDS 2016).

(iii) Forests dominated by *A. chilensis* on mesic sites (precipitation over 1000 mm year^{-1}), covering around 32.800 ha, are being partially affected by a disease called *mal del ciprés*; this disease is caused by *Phytophthora austrocedrae* (Greslebin et al. 2007) and produces gradual defoliation and mortality (Rajchenberg and Cwielong 1993; La Manna et al. 2008) (Fig. 8.14). In national parks, 40% of the total area of *A. chilensis* forests is affected by the disease (Núñez et al. 2014).

Natural invasion of *N. dombeyi* observed in diseased stands represents the opportunity to convert stands and manage them as mixed forests (Loguercio 1997; Amoroso et al. 2012).

8.5.2 Structure and Dynamic

Pure and mixed *N. dombeyi*-*A. chilensis* forests are post-fire forests (Veblen and Lorenz 1987; Veblen et al. 1996). The stands have one or two age classes, being the oldest species that have been protected from wildfires in refuges and then first recolonized the sites. *A. chilensis* is dioecious so the regeneration depends on the presence on female seed plants. The structure is often stratified into two stories (Veblen and Lorenz 1987; Dezzotti 1996), due to the different height growth rate of the species (Fig. 8.15). *N. dombeyi* grows faster early in life and reaches maximum heights first, while *A. chilensis* present a long-term lineal growth (Fig. 8.16). On the overstory of best sites, *N. dombeyi* can reach 40 m in height, while *A. chilensis* individuals in general do not exceed 30 m (on the best sites), even when they have established themselves earlier (Veblen and Lorenz 1987; Loguercio 1997) (Fig. 8.16 and Table 8.9).

Since *N. dombeyi* is not a shade-tolerant species, natural regeneration in dense stands is absent. *A. chilensis* is a little more shade-tolerant than *N. dombeyi*, so suppressed seedlings can survive for many years in the understory. However *N. dombeyi's* mortality of seedlings is mainly caused by water deficit due to competition rather than the lack of light (Caselli et al. in press). On humid sites, *N. dombeyi* regenerates in canopy gaps of 200 to over 2000 m^2 produced by treefalls (Veblen 1989). On drier sites, where it is combined with *A. chilensis*, it regenerates in canopy gaps of 400–600 m^2 (Veblen et al. 1996). On xeric sites, the regeneration *of N. dombeyi* in the gaps can be affected by extreme drought events, particularly in rocky soils with steep slopes (Suárez and Kitzberger 2008, 2010). *A. chilensis* can

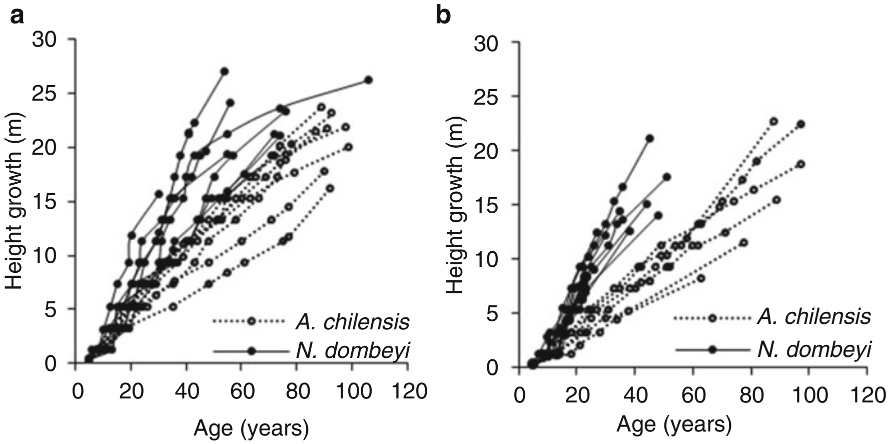

Fig. 8.15 Height growth of dominant and codominant trees (**a**) and intermediate and suppressed trees (**b**) of several mixed stands of *N. dombeyi* and *A. chilensis* located between 41°34′ and 42°00′

regenerate in smaller gaps (Fig. 8.14) and tend to be more drought resistant (Suárez and Kitzberger 2008, 2010). Pioneer species from the initial seral stage (*L. hirsuta*, *S. patagonicus*, and *A. maqui*) appear as dispersal remnants in those stands.

8.5.3 *Natural Conversion of* A. chilensis *Stands with "Mal de Ciprés" to Mixed* A. chilensis-N. dombeyi *Stands*

The release of growing space caused by the *A. chilensis* disease promotes natural regeneration (Loguercio 1997; Amoroso and Larson 2010). When mortality caused by the disease is not so high, the regeneration of *A. chilensis* predominates. But when mortality caused by the disease is higher and there are *N. dombeyi* seed trees nearby, the regeneration of this species dominates (Amoroso and Larson 2010; Amoroso et al. 2012). In the regeneration establishment phase (up to 4–5 m height), height increment of *N. dombeyi* and *A. chilensis* varies between 20 and 55 cm year^{-1} and 10–35 cm year^{-1}, respectively, depending on the canopy cover (Caselli, unpublished data). During the stem exclusion stage, *N. dombeyi* (Fig. 8.16) also achieves higher growth diameter. This is the case for all diameter classes, reaching maximum values of 8–12 mm year^{-1} and 4–7 mm year^{-1} for *N. dombeyi* and *A. chilensis*, respectively (Fig. 8.17).

The height and diameter growth result in a higher volume growth of *N. dombeyi* and an additive effect on the growth of the mixed stands (Loguercio 1997). On a given site, between age 60 and 80, mixed *N. dombeyi*-*A. chilensis* stands reach

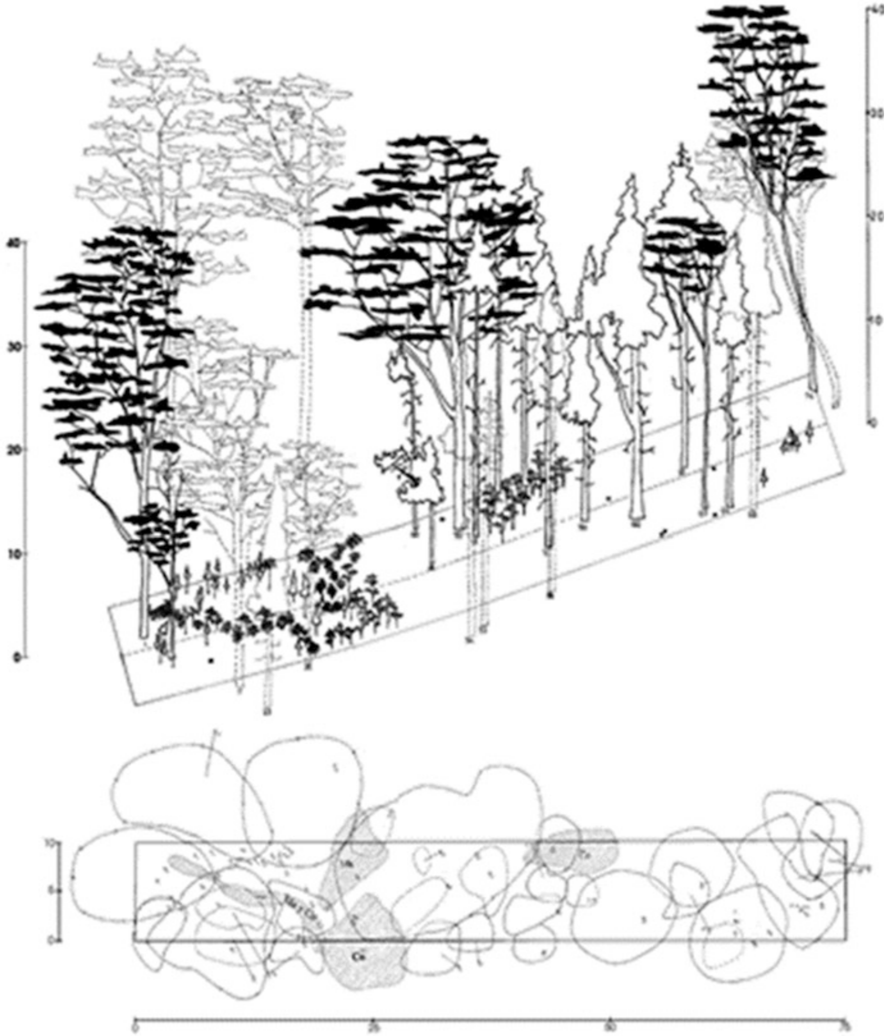

Fig. 8.16 Mixed stand profile of *N. dombeyi*-*A. chilensis* without interventions near Mascardi Lake, Nahuel Huapi National Park, Rio Negro Province, Argentina. Co, regeneration of *N. dombeyi*: Ma, *M. boaria*. Distances are in meters. Dosimetric parameters in Table 8.9

higher increments (8 and 13 m^3 ha^{-1} year^{-1}) than pure *A. chilensis* stands (4.8 and 7.5 m^3 ha^{-1} year^{-1}) (Table 8.10). In a mixed stand at “Loma del Medio-Rio Azul” Forest District (41°58′S–71°38′S), *N. dombeyi* trees sum 42% of the volume but contribute with 73% of the current volume increment (Loguercio 1997). Other stands showed the same trend (Table 8.10).

Table 8.9 Stands structural parameters of *N. dombeyi-A. chilensis* mixed forests without cuts, near Mascardi (Fig. 8.16) and Guillelmo lakes (41°20′56″S, 71°30′54″ and 41°22′47″S y 71°29′14″, respectively)

	Mascardi lake						Guillelmo lake					
Specie	Age (years)	Hd (m)	Nha^{-1}	QMD(cm)	BA (m^2 ha^{-1})	Vol. (m^3 ha^{-1})	Age (years)	Hd (m)	N ha^{-1}	QMD (cm)	BA (m^2 ha^{-1})	Vol. (m^3 ha^{-1})
N. dombeyi	76	33.3	277	45.4	44.9	747.6	49	23.6	433	35.4	42.6	525.4
A. chilensis	101	23.7	138	42.1	19.2	195.9	94	21.6	520	21.2	18.4	150.8
L. hirsuta	–	–	79	12.0	0.9	–	–		–	–	–	–
S. patagonicus	–	–	27	9.7	0.2	–	–	–	127	7.1	0.5	–
D. juncea	–	–	–	–	–	–	–	–	120	13.8	1.8	–
Total	–	–	415	39.8	64.3	943.5	–	–	1200	25.9	63.3	676.2

Age average age, *Hd* dominant height, $N\ ha^{-1}$ trees per ha, *QMD* cuadratic mean diameter, *BA* basal area, *Vol* total volume

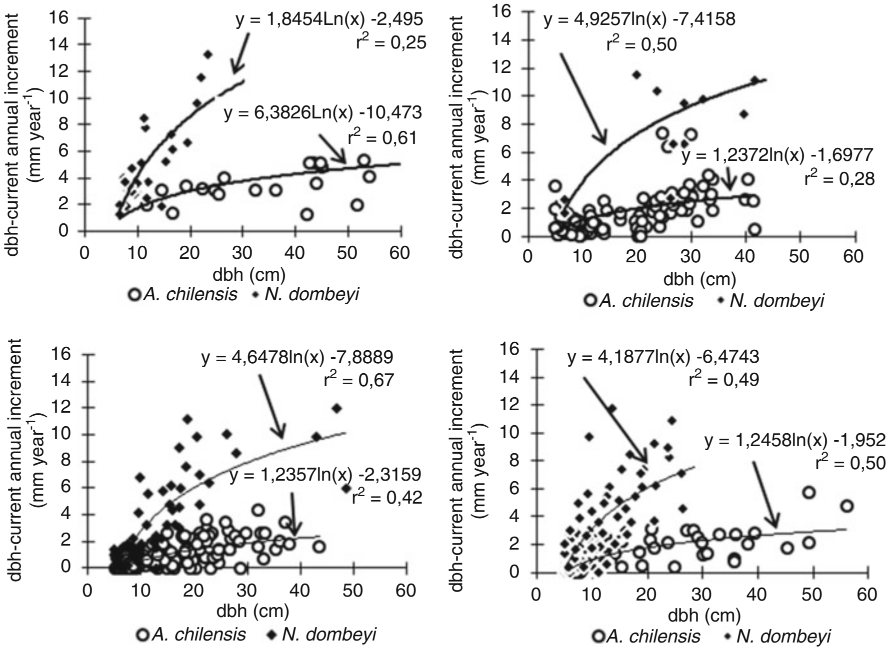

Fig. 8.17 Diameter increment of *N. dombeyi* and *A. chilensis* in four mixed permanent plots (41°58′S–71°38′S) (Loguercio 1997)

8.5.4 Toward an Adaptive Forest Management for the Mixed Forest

Management of *A. chilensis* forests depends on the presence of *mal de ciprés* disease, disturbance to which must be adapted. Although recommended sanitation cuttings (harvest of dead and severely defoliated trees) had been carried out for the last 20–30 years, they have proved to be not effective to halt the expansion of the disease. In response to that, improvement and salvage cuttings and measures to promote natural regeneration have been proposed (Loguercio 1997; Loguercio et al. 2018). Improvement cuttings consist in harvesting badly formed trees to improve stand quality. Salvage cuttings involve the removal of dead trees. Partially defoliated trees can live for many years (even decades too) and must not be removed. Salvage cuttings can produce as much as 3–4 m^3 ha^{-1} $year^{-1}$, with 3–5-year cutting cycles; volume growth of remnant trees was similar to mortality volume (Loguercio 1997). Female sick individuals that remain in the stand are important as they provide seed for natural regeneration. The establishment of natural regeneration in open stands is facilitated by maintaining some understory vegetation because it provides a favorable microclimate. As a result of this management, stand structure tends to become gradually multiaged. The intensity and frequency of cuttings are subjected to the evolution of the mortality.

Table 8.10 Structure parameters of pure and mixed *A. chilensis (Ach)* and *N. dombeyi* (*Nd*) stands at "Loma del Medio-Rio Azul" forest (41°58′S–71°38′S). (Loguercio 1997)

Specie	Age (years)	Hd (m)	N ha^{-1}	BA (m^2 ha^{-1})	QMD (cm)	Vol. (m^3 ha^{-1}) (%)	Curr. Incr. (m^3 ha^{-1} year^{-1})
Pure stands							
Ach	60	21.8	350	18.6	26.0	351	7.3
Ach	65	19.2	1157	37.0	20.2	247	4.8
Ach	83	15.2	2341	41.9	15.1	238	2.6
Mixed stands							
Ach	n.d	23.8	200	27.0	41.5	244 (84)	3.6 (53)
Nd	n.d	14.8	440	6.5	13.7	45 (16)	4.0 (47)
Total			640	33.5	25.8	289	7.6
Ach	n.d.	20.4	850	39.3	18.3	290 (69)	1.3 (14)
Nd	n.d.	21.3	120	11.4	34.2	128 (31)	7.7 (86)
Total			960	33.1	21.0	418	9.0
Ach	64	19.1	1200	36.5	19.7	251 (58)	3.4 (27)
Nd	39	23.7	590	16,2	18.7	182 (42)	9.3 (73)
Total			1790	52.7	19.5	433	12.7
Ach	n.d.	23.6	550	37.4	29.4	325 (65)	3.1 (24)
Nd	n.d.	21.2	760	17.5	17.1	177 (35)	9.6 (76)
Total			1280	44.9	20.1	502	12.7

Hd: dominant height; N ha^{-1}: trees per ha; BA: basal area; QMD: quadratic mean diameter; Vol.: total volume; Curr. Incr.: volume current increment

In mixed *N. dombeyi*-*A. chilensis* stands where *mal del ciprés* is present, regeneration of *N. dombeyi* can enhance productivity and produce high-quality timber representing an opportunity to develop a more intensive silviculture (Loguercio 1997; Loguercio et al. 2018). There is not much information about management of mixed *N. dombeyi*-*A. chilensis* affected by *mal del ciprés*, but current knowledge about growth and dynamics of these forests would make it possible to elaborate the first silviculture guidelines. Treatments should consider the conversion of pure disease *A. chilensis* into mixed structures and its subsequent conduction to regulate its composition and density. Since *N. dombeyi* outgrows *A. chilensis* (Tables 8.9 and 8.10, Figs. 8.16 and 8.17), to control composition and growth of mixed stands, it is convenient to keep species in separate groups rather than in a uniform mixture. The area assigned to each species will depend on the management objective. Group selection methods are considered appropriate for the regeneration of *N. dombeyi*, with final gaps of approximately 500–1000 m^2. However, on xeric sites gaps should be open only where advanced regeneration is present, and they should be expanded gradually, in two or three entries, every 5 years. This would also be recommended where the diseased *A. chilensis* trees occur in groups. Established regeneration, that is, when they reach 4–5 m of height, would be achieved in 10–15 years. Then a cleaning cut to favor the best saplings should be applied. Along the stem exclusion stage, two to three thinnings should be carried out before the final cut to be done when DBH reaches 45–50 cm. The nicest *N. dombeyi* trees could eventually be pruned to produce clear timber.

In places within the stands where *A. chilensis* is to be maintained as the main species, the same management guidelines as for pure forests can be applied. To maintain the stand composition, *N. dombeyi* seedlings should be removed before they reach 3–5 m of height, except for a few with very good form and vigor.

When natural regeneration does not prosper, reforestation of one or both species can be carried out. Gaps and stripes, with an area less than 350 m^2, have resulted in high initial survival (>80%) for both species (Pafundi et al. 2014). On mesic sites (±1000 mm $year^{-1}$), *A. chilensis* and *N. dombeyi* plantations with the presence of diseased *A. chilensis*, canopy cover values between 30% and 75% favor the initial survival of both species. On xeric sites (<700 mm $year^{-1}$), this protection effect is more pronounced.

8.6 Concluding Remarks

Mixed temperate forests of South America are found south of 33°S, most of them west of the Andes Mountains. East of the Andes, mixed forests are small ingressions from the west and transitions between pure forests types of mesic and xeric sites.

Forest management of evergreen forests west of the Andes, with their great variety of species (more than 20 per ha, mostly hardwoods), with different behavior, growth rates, and timber quality, represents the greatest challenge. Some options have been presented for this forest type, considering even- and uneven-aged silvicultural systems. For old-growth forests, uneven-aged silviculture is proposed by means of the selection cutting system oriented to shade-tolerant and midtolerant species with a large life-span. It is estimated that tree growth can be doubled with this management. Nevertheless, the model should be consolidated through its proper implementation and monitoring, in operational management cases.

Secondary mixed forests in Chile also present a great variety of species composition, reproduction forms, and development states that, depending on sites, enable different management models to apply. Management outlines for even- and two-aged forest types with one or two strata and the presence of intolerant, midtolerant and/or shade-tolerant species have been presented. In general the examples indicate the convenience to initiate the reduction of the density at an early age, orienting the management to more valuable species. The decisions to conduct cuttings for the main species are made by means of available density diagrams and density equations.

Mixed secondary forests of *Nothofagus* spp., known in Chile as “renovales,” predominate in the stem exclusion phase with ages between 60 and 80 years. There, management decisions are made according to the presence or absence of shade-tolerant and midtolerant species and stand stocking. The management aims to combine the value production of the *Nothofagus* and to favor the development of the midtolerant and shade-tolerant species of the second stratum for its future production. Thinnings are also defined using available management density diagrams.

East of the Andes, in Argentina, mixed *Nothofagus* forests do not present the tolerant and semi-tolerant shade species of the evergreen forest type, due to the humidity threshold. These forests predominate in the old-growth and reinitiation stage. Hence, forest management is done with a shelterwood system. Its successful implementation, with achieved regeneration on approximately 1000 ha along more than 25 years in the reserve area of Lanín National Park, is an outstanding example of effective silvicultural management in the subantarctic forests from Argentina. It has been observed that young *Nothofagus* stands, even though its growth rate is smaller than the most humid zone in Chile, respond to thinnings with an increment in volume, even with 40–60 years of age.

Xeric conditions reduce tree diversity, predominating pure forests. The climatic rigorousness that predisposes the occurrence of stress in the trees due abiotic and biotic damages, including the potential effects of climate change, suggests an approach of adaptive management. For example, the *A. chilensis* forests affected by *P. austrocedri*, where the regeneration of *N. dombeyi* is invading, present the opportunity to convert it to mixed forests. *N. dombeyi* increases the stand productivity, broadening the possibility of a more intensive silviculture, in comparison with the pure and diseased *A. chilensis* forests. Due to the greatest growth of *N. dombeyi*, its stocking in the stand must be regulated to allow *A. chilensis* to grow successfully.

Overall, there is a considerable knowledge about ecology, dynamics, and silviculture for a sustainable management of mixed temperate forests of South America. However, effective forest management in a large scale is not yet applied, being this the major pending challenge for the forestry sectors of Chile and Argentina.

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Chapter 9
Mixed Forest Plantations

Jon Urgoiti Otazua and Alain Paquette

Abstract Forest plantations have become increasingly important worldwide. Whereas the global forest area is reduced every year, the establishment of forest plantations is experiencing a notable increase in the last decades. This trend also brings an increase in the dependence of society on forest plantations to obtain both timber and non-timber services. However, currently, the vast majority of forest plantations are composed of monospecific stands under the premise that they facilitate and maximize the harvesting of a few desirable tree species. As informed by biodiversity-ecosystem functioning science, these species-poor plantations may alter negatively the quality of ecosystem functions and services that humankind obtain from them. In addition, both forest plantations and natural forests are facing unprecedented ecological disturbances driven by global change as well as socio-economic uncertainties. This calls for a novel long-term forest management which seeks to provide tree plantations that are more resistant and resilient as well as able to adapt to these changes in social and environmental conditions. We argue that mixed plantations are the best option to meet these goals, since mixed-species stands support species with different biotic and abiotic sensitivities and recovery mechanisms following disturbances, thus ensuring the ability to self-organize, increasing resilience and adaptive capacity. In this chapter, we review a list of socioecological uncertainties and risks that forest plantations may face and how more diverse plantations can better cope with them compared to monocultures while stabilizing productivity or helping fight global warming through carbon sequestration.

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9.1 Introduction

Planting trees has a long history, certainly as far back as ancient civilizations. The first planted forests were presumably established near human settlements to provide firewood, food, medicine and other goods. But plantation forestry, as we understand today, did not start until trees were planted as a way of regenerating forests and for the afforestation of bare lands. These first forestry activities originated in Europe in the seventeenth century mainly to satisfy an increasing appetite for wood following the industrial revolution. It should be mentioned that at that time large forest plantations for other non-timber services were also established, although globally to a lesser extent (e.g. dune stabilization in the Landes forest in 1801). Single-tree species plantations seemed like the simplest way to achieve a fast and efficient wood production, and since in the society of the time an awareness of biodiversity was not extended, tree plantations were well accepted and even promoted as a way to improve upon the natural world by concentrating primary production into one product (desirable timber) while maintaining tree cover for other uses such as hunting, food gathering and so on. Over time, foresters started adopting fast-growing exotic tree species or hybrids in different parts of the world to improve wood production rates, so much so that many countries now produce most of their lumber from such monospecific exotic tree plantations.

Forest plantations have become increasingly important worldwide. Forest losses in 2010–2015, most of which were natural forest, were offset partially by the establishment of planted forests with an average annual growth of 3.1 million hectares per year (FAO 2015). According to the Food and Agricultural Organization of the United Nations (2015), the total global area of forest plantations in 2015 was estimated to be 291 million hectares, corresponding to 7% of all forested area. While it is true that the objectives for establishing plantations are now more varied, producing the most wood as cheaply and quickly as possible is still generally the most important. The FAO estimates that 76% of forest plantations are established primarily for wood production and that about 25% use exotic species. Despite occupying a relatively small area, forest plantations already effectively provide more than half of the world's demand for wood, and some estimations predict that by 2050, plantations will produce 75% of all roundwood in the world (Sedjo 2001). The incessant increase in world population makes countries increasingly dependent on forest plantations to satisfy the demand, often in conjunction with the degradation and destruction of natural forests. Therefore, it seems evident that the global wood supply is shifting from natural forests to planted forests (FAO 2010).

Hence, it is perhaps not surprising that forest plantations have developed a bad reputation among conservationists. The increased concern about the loss of biodiversity by society in recent times often associated with the increasing loss of natural forests and the development of industrial large-scale monoculture plantations generates widespread rejection among population. Plantation forests have been called "biological deserts" (Stephens and Wagner 2007), and some even argue that "plantations are not forests" (Carrere 2004). This bad reputation is often deserved but just as often misinformed (Paquette and Messier 2010). While most forest plantations are established only for the production of industrial wood, plantation forestry designed to provide multiple ecosystem services can restore some ecological services provided by natural forests when established on previously degraded land and can even reduce pressure on natural forests when incorporated into integrated landscape management, known as "forest functional zoning" (Messier et al. 2009; Côté et al. 2010). Under this management, a certain proportion of the land is allocated primarily to timber production and intensive silviculture, while conservation efforts can focus on other areas dedicated to extensive management and strict conservation**.** They can also play a key role in the fight against global warming, through carbon sequestration.

Due to the ongoing increases in the size of the plantation globally (FAO 2010) and acknowledging the fundamental role they may play ecologically and socio-economically now and in the future, a novel management will be required to ensure these areas play useful conservation and ecosystem service roles (Lindenmayer et al. 2015). In this regard, Lindenmayer et al. (2015) argued to view tree plantations as novel ecosystems (sensu; Hobbs et al. 2006), thus acknowledging that they are not "natural" ecosystems but non-native or native tree species assemblages that are deliberately established and that often support novel assemblages of species and habitats and can sometimes make important contributions to conservation (Lindenmayer et al. 2008; Valentine and Stock 2008). Considering tree plantations as novel ecosystems can free forest managers and policymakers from viewing them as a simplified system of the natural forests and help them to better deal with the challenges and opportunities associated with plantations (Lindenmayer et al. 2015).

The limitations of today's widespread management, by which forest managers see plantations as stable and predictable systems, are appreciable since both the social and ecological dimensions and certainties on which it is based change continuously (Messier et al. 2015). Plantations are constantly affected by global changes such as climate warming, exotic species invasions, pollution, socio-economic factors and the changing needs and perceptions that humans have regarding tree plantations. The health of plantations, just like natural forests, is more heavily threatened at present than ever before (Boyd et al. 2013; Santini et al. 2013; Roy et al. 2014). For instance, it is expected that forests and plantations of Central Europe will increasingly be affected by novel pests, such as the Asian longhorn beetle (*Anoplophora glabripennis*) (Krehan 2008) and the pinewood nematode (*Bursaphelenchus xylophilus*) (Mota et al. 1999) which may have devastating consequences both ecologically and economically (Soliman et al. 2012; Faccoli and Gatto 2016). Plantations now must not only be analysed through their timber production yield, but it is also necessary to evaluate their ability to provide other non-timber products and services and their capacity to face the uncertainties and risks that characterize both the natural environment and the market (Carrere 2004). Indeed, who can predict if the plantations that are standing today will be profitable economically in 50 years? Who can quantify accurately the risks associated with environmental disturbances (extreme weather conditions, invasive pests) over that period? For instance, climate projections suggest that summer temperatures in France and on the Iberian Peninsula may increase by 6 °C or more by the end of the twenty-first century compared with the 1961–1990 reference average (EEA 2010; IPCC 2007) which will have unpredictable impact on forests and tree plantations. These changing, and increasingly uncertain, socioecological conditions call for the development of a novel long-term forest plantation management which seeks to provide tree plantations that are (1) more diverse both in species and structurally, (2) better integrated at landscape level with other forest elements, (3) more resilient and resistant and (4) able to adapt to the rapidly changing social and environmental conditions. In this regard, this new breed of tree plantation management may have a lot in common with the complex adaptive system approach with emphasis on the adaptive capacity of ecosystems while acknowledging that uncertainties are inevitable (Puettmann et al. 2013).

Based on the notion that homogenous products are cheaper to produce and manipulate, management practices have typically led to even-aged, monospecific or species-poor stands (Puettmann and Ek 1999; FAO 2010; Paquette and Messier 2010). Whereas monocultures have excelled at providing large quantities of wood, this has often come at the expense of biodiversity (Lindenmayer and Franklin 2002), with resultant implications for additional ecosystem services and resilience (Jactel et al. 2009; Griess and Knoke 2011). For example, in Central Europe, after some unexpectedly devastating storm events such as “Lothar” (Central Europe 1999), “Kyrill” (Germany and Slovakia 2007) and “Klaus” (France and Spain 2009), large extents of plantations were destroyed, most of which were even-aged monospecific conifer stands of Norway spruce (*Picea abies*) or maritime pine (*Pinus pinaster*). The ecological and economic consequences were dramatic. Although it is known that some species such as Norway spruce are more vulnerable to windthrow than others (Lindner et al. 2008), a more diverse and structurally more heterogeneous canopy is likely to be more resistant to windthrow. In this context, the planting of mixtures of species seemed to have prevented massive damage and to have increased single-tree windthrow rather than whole-stand blowdowns.

This example illustrates the need to design more diversified forest plantations which can continue to provide high yields of timber as well as an array of other ecosystem services, while being more resistant and resilient to disturbances. In this chapter we will discuss the potential of mixed plantations to meet resilience, resistance and adaptability objectives.

The concept of resilience in ecological systems was introduced by Holling (1973) in order to describe the persistence of ecosystems in the face of changing environment variables. Later, Holling (1996) defined resilience in two different ways: (1) *engineering resilience* which is defined as the speed with which an ecosystem returns to a previous equilibrium state following a disturbance and (2) *ecological resilience* which refers to the amount of disturbance that a system can absorb before the system changes its structure and functioning. This definition assumes the possibility a system can flip to another stable state after a disturbance.

The definition of resistance describes the property of systems to remain “essentially unchanged” when subject to disturbance. That is, it is the capacity of a system to absorb disturbances while not changing its structure and functioning.

Adaptability is the capacity of a system to adjust its structure, composition and interactions in response to external forces. Adaptability in a forest management context would rely on implementation of practices that ensure an ecosystem continues to provide equivalent goods and services even as it changes in response to external forces (Puettmann et al. 2013).

9.2 Managing Diversity: Tree Plantations

The potential of natural forests to adapt to unpredictable events and risks is limited by their biological restrictions (Travis 2003). In contrast, the adaptive potential of tree plantations is far greater as forest managers can modify silvicultural regimes and tree species composition to maintain the productive and thus economic capacity of these forests to adapt to, or mitigate, the effects of global socioecological changes. Forest managers will have to adapt management practices over time to changing environmental conditions in order to remain stable and retain the capacity to continuously provide multiple ecosystem products and services (Puettmann et al. 2013). Tree plantations used to be located near human settlements for economic reasons; therefore, changing the way we manage plantations can have profound and rapid impacts on the social acceptance of forestry practices (Paquette and Messier 2013). However, these forest plantation management changes must be made through a science-based approach to decision-making, assessment and planning. We must first review recent developments in ecology, regarding the role of diversity in the functioning of ecosystems. In this review, we will show that increasing levels of diversity at both stand and landscape scales are best in designing more resistant, resilient and adaptable plantations while providing important ecosystem services.

9.2.1 Biodiversity-Ecosystem Functioning Theory

Managing for diversity rests on the assumptions that diversity leads to greater stability of forest ecosystems and reduced management risks. Mixed stands are indeed more resistant to various forms of damage and more diverse in their fauna and flora composition, than pure monoculture stands (Spiecker 2003). Low-diversity systems, such as monocultures, may also be less resistant and resilient to natural disturbance (Drever et al. 2006) or pests (Jactel and Brockerhoff 2007), something that global change might exacerbate (Woods et al. 2005). From the point of view of productivity, several studies provide evidence that biomass production can improve with tree diversity (Nadrowski et al. 2010; Scherer-Lorenzen 2014).

In the last two decades, much research has been carried out to explain the role that biodiversity plays in promoting healthy ecosystem functioning such as productivity but also adaptive capacity, resilience and resistance (Symstad et al. 2003; Reiss et al. 2009; Loreau 2010). The interpretation of these studies, however, has been controversial because two types of mechanisms may operate in combination for generating positive diversity (Tilman et al. 1997): (1) *the complementarity effect* and (2) *the selection effect* (Loreau 1998). The complementarity effects include niche partitioning, positive interactions (i.e. facilitation) and positive feedbacks or resource supply, whereas selection effects are due to dominant species driving ecosystem functioning (Roscher et al. 2012). The selection effect may be important for plantations and should be accounted for when choosing species for planting in mixtures. In addition to these two mechanisms, it has been hypothesized that more diverse plantations possess a better self-regulation and adaptive and resistance capacity; (3) *the insurance hypothesis* (Yachi and Loreau 1999) proposes that diverse plant communities probably cope better with, or recover more quickly from, changing conditions such as unpredictable stress, disturbance or climate change, than less-diverse communities (Griffin et al. 2009; Van Ruijven and Berendse 2010). This hypothesis suggests that in a functional group (i.e. collection of species sharing important ecological characteristics and playing an equivalent role in the community), formed by many species, species often manifest functional redundancy (Walker 1992). These species, in turn, may show asynchronous responses to environmental changes or display a phenomenon of time niche differentiation (Elmqvist et al. 2003) which may help to enhance the community's adaptability and resistance to change (McCann 2000; Laliberté et al. 2010). These differences in response to environmental change within a functional group increase the probabilities that one species could take over the role of another redundant species that does not survive the disturbance or new conditions because of functional redundancy (Walker et al. 1999; Yachi and Loreau 1999).

9.2.2 Biodiversity-Ecosystem Functioning Applied to Tree Plantations

Field experiments and meta-analysis of plantation trials have confirmed the positive effect of diversity on productivity (Potvin and Gotelli 2008; Zhang et al. 2012). Also, tree diversity experiments such as BIOTREE (Scherer-Lorenzen et al. 2007) and IDENT (Tobner et al. 2016), both members of the TreeDivNet (Verheyen et al. 2015; Paquette et al. 2018), have confirmed these positive relationships (Grossman et al. 2018). Mixed-species tree plantations may indeed be more productive than monocultures, essentially by allowing for a more optimal use of resources (Zhang et al. 2012).

Possible mechanisms have been deciphered that would confer overyielding in mixed plantations: (1) complementarity in the resource supply through the development of the stratification of the canopy. Williams et al. (2017) observed that the spatial complementarity of tree crowns in mixtures was strongly and positively related to functional diversity and to stem biomass overyielding. (Sapijanskas et al. 2014) also showed that more diverse stands enhance community-level light captures increasing tree growth through crown architectural differences. (2) Facilitation in the nutrition of a valuable timber species growing in mixture with a nitrogen-fixing species. The positive interactions among species, where certain species improve environmental conditions for others or supply a critical resource such as nitrogen through fixation, have been documented for fast-growing *Eucalyptus* interplanted with nitrogen-fixing tree species, often *Acacias*, or Douglas-fir (*Pseudotsuga menziesii*) with red alder (*Alnus rubra*). Pretzsch et al. (2010) also documented overyielding in natural mixtures of Norway spruce and European beech (*Fagus sylvatica*).

In addition, well-planned mixed plantations can emulate natural stand development, even in high-input intensive management. For example, crops can be grown in the understorey, or some fast-growing species can be harvested earlier than slower-growing species to generate an early return (Paquette et al. 2008; Rivest et al. 2009). Plantation designs like this may be more resistant to insect outbreaks or diseases than monocultures (Drever et al. 2006; Jactel and Brockerhoff 2007) reducing the associated risks (Hartley 2002) in accordance with the *insurance hypothesis*. However, temporal dynamics is a dimension that is not usually taken into account in diversity-resistance relationships. Whether these relationships are present over the longer term or only temporarily is an important question that needs more investigation. Although important progress has been made, recent studies that tested the diversity-resistance relationship in forests have shown both negative and positive effects of diversity in long-term resistance (Grossiord et al. 2013a, b; Paquette et al. 2017). Therefore, it is important to better understand how tree diversity may reduce damage in the long term, at least for a plantation rotation, and to assess the overall benefit at the time of harvesting (Jactel et al. 2017).

In conclusion, forest managers may benefit from planting mixed plantations in the ways documented in biodiversity-ecosystem functioning (BEF) science. (1) Mixed plantations could be more productive than monocultures through facilitation and complementarity but also from a well-planned design including highly productive species (selection effect). (2) Mixed plantations may have a greater capacity to adapt to unpredictable events and risks while maintaining ecosystem functions. Indeed, mixed plantations, even if not always more productive than the single best monoculture for a given site, should be better able to cope with the multiple challenges increasingly expected of them, both for societal (cultural, economic) and environmental (stability facing global change) reasons. In designing forest plantations with multiple objectives in mind, and accepting that both environmental and socio-economic conditions are dynamic and uncertain, managing for diversity may help provide a more resistant, resilient and adaptable forest plantation while stabilizing timber production.

9.3 Mixed Plantations: Resistance, Resilience and Adaptability Against Uncertainties and Risks

Future uncertainty is a major issue in developing long-term forest plantation management strategies and needs to be taken into account explicitly in decision support. The magnitude and effects of climate change on forest ecosystems and on management strategies are subject to continuous uncertainty. Not only is the climate changing but also societal demands for goods and services from forests. Some studies indicate that societal preferences and values can change drastically within short periods (relative to forest management cycles), altering the social environment for management (e.g. Johnson and Swanson 2009). This is a key challenge for forest managers, as they must deal with novel phenomena and multiple trade-offs (Felton et al. 2016). Can we manage forest plantation without compromising much on present and future productivity, or better yet, while increasing temporal stability (thus predictability) in yield? Planting mixed plantations seems to be the best option to meet these goals, since mixed-species stands, functionally more diverse than monocultures, support species with different biotic and abiotic sensitivities and recovery mechanisms following disturbances, thus ensuring the ability of ecosystems to self-organize, increasing their resilience and adaptive capacity (Messier et al. 2015). However, tree plantations and the strategies to manage them are diverse, with each plantation featuring different tree species composition, ecological conditions, management goals, risks and societal demands for good and services. Therefore, adaptive management strategies must be developed in different ways depending on the socioecological conditions. Here, we show a list of risks and uncertainties that tree plantations will face with and how more diverse plantations can cope better with them compared to monocultures.

9.3.1 Mixed Plantations for Facing Biotic Disturbances

9.3.1.1 Mixed Plantations Facing Pests and Pathogens

Relative to monocultures, the use of mixed-species stands may be expected to be more resistant reducing the risk of pest and pathogen outbreaks (Pautasso et al. 2005; Jactel et al. 2009). This hypothesis is supported by two meta-analyses which demonstrate that a particular host tree species is less vulnerable to damage by a given pest insect when grown in mixture rather than in monoculture (Jactel and Brockerhoff 2007; Castagneyrol et al. 2014). Liu et al. (2015) also showed that the effect of soil-borne pathogens depends on the abundance of host tree species, being more harmful when host tree species density was high than when its density was low. In this context, reducing the proportion of susceptible trees affecting the pathogen or pest-host encounter and transmission potential or admixing disease-resistant species to reduce the root contact between vulnerable species can reduce damage rates

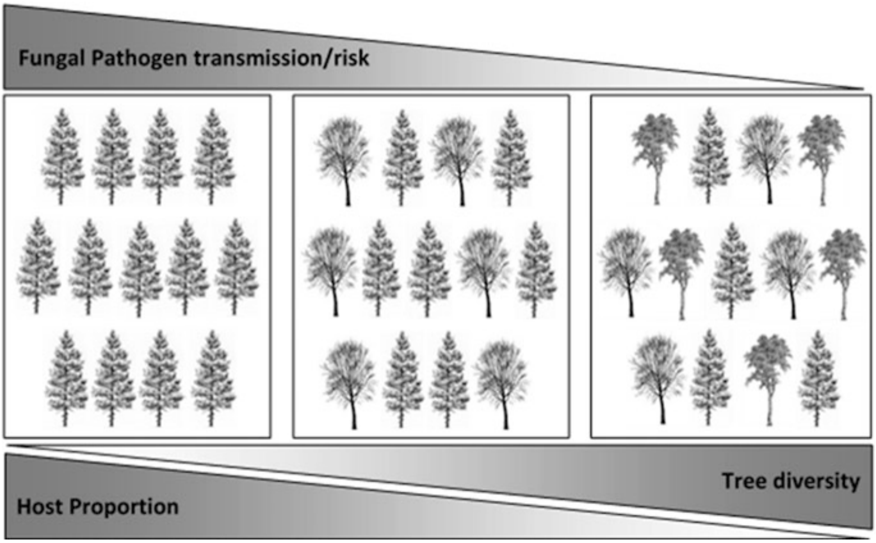

Fig. 9.1 Graphical illustration of the effect of tree diversity among neighbouring trees on fungal pathogen transmission (Adapted from Hantsch et al. 2014). Fungal pathogens of a target host tree (here a conifer) are expected to decrease with increasing tree diversity from left (monoculture) to right, where the vulnerable species is diluted, leading to a reduction of the overall risk

(Lindén and Vollbrecht 2002; Keesing et al. 2006; Barbosa et al. 2009; Hantsch et al. 2014) and, therefore, provide more resistance to the community (Fig. 9.1). For example, in Sweden, the risk of damage by the most destructive pathogen affecting spruce, *Heterobasidion annosum*, may be reduced by admixing pine (Korhonen et al. 1998).

Alternatively, increased tree diversity can have a direct or indirect positive effect on the abundance and diversity of the natural enemies of pest species (Underwood et al. 2014). Pest outbreaks may be reduced by increasing the presence of their predators or parasitoids acting as control species (Jactel et al. 2009). In this context, the addition of pine to a stand may reduce damage on conifer stands by increasing the abundance of predatory ants (Koricheva et al. 2006) which may control pest species such as the pine weevil (*Hylobius abietis*) (Maňák et al. 2013). On the other hand, volatiles from non-host plants interfere with the host-finding ability of specialized insect herbivores when searching host species (e.g. Jactel et al. 2011; Zhang and Schlyter 2004). For example, spruce bark beetle damage can be reduced by adding birch to the stand, as the volatiles from these non-host tree species can help deter spruce bark beetles (Zhang and Schlyter 2004).

Nevertheless, although mixed plantation may reduce the risk of pest and pathogen damage, some considerations must be taken before planting. On the one hand, the addition of a given tree species may itself be susceptible to pests or pathogens at a given location. On the other hand, although mixtures may be more effective at coping with specialized pathogens, damage by generalist species may increase

(Plath et al. 2012). To avoid this, a vulnerability assessment of the tree species used in the plantation to reduce risks is recommended. However, outcomes are dependent on the specific sites' conditions and on the mixed-stand characteristics (Vehviläinen et al. 2006; Castagneyrol et al. 2013). This means that even if there is enough evidence that mixed plantations may cope better with damage of pests and pathogens, large uncertainties still remain, so that unexpected negative outcomes are possible.

9.3.2 Mixed Plantations for Facing Abiotic Disturbances

9.3.2.1 Mixed Plantations Facing Windthrows

Wind damage is one of the most important and widespread disturbances to forests and plantations. For instance, in Europe, storms are the most important damaging factor and are responsible for more than half of all the damage recorded (Schelhaas et al. 2003). While it is true that some species are more susceptible to windthrow than others (Lindner et al. 2008), some studies demonstrate that mixed plantation may cope better against windthrows (Schütz et al. 2006; Valinger and Fridman 2011). Lüpke and Spellmann (1999) analysed the susceptibility of some commercially important tree species to storm damage and found that Norway spruce (*Picea abies*) is ten times more vulnerable to windthrow than European oak (*Quercus robur*) and sessile oak (*Q. petraea*) and approximately four times more than European beech (*Fagus sylvatica*). The susceptibility of conifers such as Norway spruce to disturbances is mainly a consequence of their shallow rooting systems and needle retention during wintertime, when the storms occur (Knoke et al. 2008). An active adaptation of forest plantations to face the risks and uncertainties associated with windthrows includes the introduction of tolerant species (native as well as introduced species or provenances) that are potentially better adapted to these conditions, conferring more resistance and adaptability to the community. Some studies have provided clear evidence that mixed stands of coniferous with broadleaves tree species develop a higher resistance to windthrow compared to pure conifer stands (Schütz et al. 2006; Valinger and Fridman 2011). Dhôte (2005) also showed that mixing spruce with tree species such as birch or pine, which are considered to have higher mechanical stability (Peltola et al. 2000), could improve the overall wind stability of stands compared to pure spruce stand.

9.3.2.2 Mixed Plantations Facing Fire Risks

Climate change is expected to bring drier summers which increase fire frequency and intensity (Bond et al. 2005; Peterson et al. 2005; Flannigan et al. 2006; Van Der Werf et al. 2008). In addition to heat sources and weather conditions (wind, air humidity), the relative susceptibility of a forest to fire will depend on the availability of fuel, fuel composition and its distribution within the stand (Schelhaas et al. 2010). All these factors are strongly determined by tree species composition (Jactel et al. 2009). In general, tree species with a foliage of high contents of resins and oils such as conifers and eucalypts are more flammable than that of most deciduous broadleaved tree species (Dickinson and Johnson 2004; Michaletz and Johnson 2007). Many studies have provided enough evidence that mixtures of conifers and broadleaves are less vulnerable to fire than pure conifer stands, where in mixtures fires tend to be of lower extend and intensity (Kafka et al. 2001; Wang 2002; Gonzalez et al. 2006; Silva et al. 2009). The presence of fire-resistant trees in a mixture may provide a physical barrier, limiting flame propagation, thus preventing ignition of neighbouring less-resistant trees (Azevedo et al. 2013). For instance, many eucalypt species and some oaks such as *Quercus suber* are characterized by thick bark which provides more resistance to fire. Also, the presence of species which have developed a range of structures and mechanisms to postfires may provide more resilience to the stand. Thereby, seeder and resprouter species may enhance the capacity of the stand to regenerate after a fire.

Nevertheless, when managing a mixed plantation, one should try to analyse or predict how the plantation will respond to a fire, since its degree of resistance will be the result of a complex set of interactions between species of different physiological and morphological characteristics. For example, a mixed plantation design may increase light interception, limiting the development of understorey vegetation, which decreases the intensity of fires. As an example, mixing species with high shade tolerance and light-demanding species may reduce the development of understorey and thus levels of fuel. Also, mixture canopy with a high leaf area may provide a higher relative humidity of the air beneath the canopy and therefore higher fuel moisture content and lower flammability (Bauhus et al. 2017; Jactel et al. 2017) conferring higher resistance to the stand against fire. Conversely, mixture stands with high density of fuel ladders may increase the probability of crown fires in species that would otherwise not or rarely experience these (Bauhus et al. 2017).

9.3.2.3 Mixed Plantations Facing Droughts

In the context of climate change, expected drier and warmer environmental conditions will have drastic consequences on forest ecosystem functioning and mortality (e.g. Allen et al. 2010). In a mixture, species interactions may help reduce water stress, through facilitation or complementarity in soil water uptake and use (Forrester and Bauhus 2016). Nevertheless, interestingly, Paquette et al. (2017) found an overall negative relationship between tree diversity and the capacity of stands to maintain productivity faced with temperature divergences (i.e. warmer conditions). This could be the result of the interactions between different species which could lead to an increase in evapotranspiration rates (Kunert et al. 2012), inducing higher water stress under drought conditions. However, these results contradict previous studies which found positive effects of diversity during dry (vs wet) years (Grossiord et al. 2013a, b) or in drought-prone environments (Grossiord et al. 2014).

Interestingly, although (Grossiord et al. 2013b) showed that the water use efficiency in mixed stands was much higher than in monocultures during dry years, this did not translate into the observed reduction in productivity along biodiversity gradient with drought. This suggests that mixed stands exploit more intensively soil resources which may lead to negative biodiversity effects where soil water can be more exhausted during drought periods by mixtures (Grossiord et al. 2013b).

In summary, it seems that, although it is true that mixed stands are capable of exploiting water more efficiently than pure stands, in prolonged droughts this can turn against them to make them less productive and more vulnerable compared to low-diversity stands.

9.3.3 Mixed Plantations and Socio-economic Disturbances

Natural forests and tree plantations are essential to humankind as they provide a wide variety of social and economic benefits (FAO 2010). Unfortunately, the current loss of biodiversity is threatening the functioning of these ecosystems and thus the services that society obtains from them. Forestry practices typically simplify nature toward even-aged, monospecific or species-poor stands to facilitate and maximize the harvesting of a few desirable tree species (Puettmann et al. 2009) which drastically affect biodiversity. Consequently, these simplified systems may be more vulnerable to collapse (i.e. an abrupt and undesirable change in state), in the face of biophysical risks as well as the market (Nagaike et al. 2006). For example, the establishment of monospecific conifer plantations over the past 50 years in Japan is now on the verge of collapse due to increasing competition from cheaper imported timber and because of high harvest labour costs (Nagaike et al. 2006). Many of these plantations are problematic because they were not designed to self-regulate and adapt to future uncertainties in the absence of a regular human intervention. Planning tree plantations that are able to self-regenerate and adapt if left unmanaged is an important precautionary approach (Lindenmayer et al. 2015).

Conserving biodiversity is essential for reducing the risks of forest ecosystem collapse (Macdougall et al. 2013), since biodiversity plays critical roles in ecosystem functioning, dynamics and stability (e.g. Reich et al. 2012). While mixed plantations may need additional considerations, and are likely to increase the costs of management and harvesting (Bauhus et al. 2017), their improved adaptive capacity to uncertainties and risks may still result in overall improved financial security and net benefits in the long term (Knoke 2017). Moreover, the economic returns from mixed plantation may be less sensitive to fluctuations in timber prices than monospecific stands, and therefore the financial risks may be lower (Knoke et al. 2005). Finally, the diversification of harvesting times may also serve as an effective mechanism against volatile timber prices (Knoke et al. 2001). It allows forest managers to adapt their commercial thinning regimes depending on the market value of tree species that make up the plantation (Lu and Gong 2005).

On the other hand, forest management also requires flexibility and adaptability in terms of societal demands and values (e.g. carbon sequestration, air purification, water quality, aesthetics and food) (Messier et al. 2015). These societal preferences can change drastically over short periods (relative to forest management), radically altering the social environment for forest management (e.g. Johnson and Swanson 2009). This calls for planning forest plantations under an ecologically sustainable management to maintain the forest structural complexity, species diversity and composition and a diversified ecological process and function (Lindenmayer et al. 2012). Thus, planting mixed plantations together with a sustainable forestry practices (i.e. retention approach) may cover social needs and demands more efficiently than monospecific stands.

9.4 Can Mixed Plantation Stabilize Temporal Productivity?

Disturbances may remove a significant amount of biomass through mortality of trees which have direct consequences on productivity. As we have seen, mixed plantations may be more resistant and resilient to different disturbances than monocultures (Woods et al. 2005; Jactel et al. 2009). However, the direct impacts of disturbances on productivity are not well quantified, mainly because of the difficulty to capture both variation in disturbance and the whole recovery period after disturbance (Bauhus et al. 2017). In addition, different disturbances can act synergistically, which makes it difficult to analyse the real effect of a particular event on productivity (Bauhus et al. 2017). Nevertheless, disturbances such as a single drought event which do not cause widespread mortality, but rather cause a variation in productivity, allow testing whether tree diversity can stabilize productivity over time (e.g. Jucker et al. 2014).

Stability of productivity refers to how much productivity fluctuates around its long-term mean over time (Tilman 1999). This stability is measured as the ratio between the mean productivity (μ) and the standard deviation (σ) over time. Recent studies suggest that tree diversity may stabilize productivity over time and contribute to a reduction in stress through a combination of three mechanisms by which the interannual fluctuation in productivity decreases as diversity increases (Hector et al. 2010; del Río et al. 2014; Hautier et al. 2014; Jucker et al. 2014). (1) *Overyielding* has been shown to promote stability by increasing μ in grasslands (Hector et al. 2010) and in forests (Jucker et al. 2014) through niche partitioning and decreased competition among different species (Loreau and Hector 2001). However, del Río et al. (2017) showed that despite they found a significant overyielding at the community level, this overyielding did not promote temporal stability. Nevertheless, it is important to mention that this study was carried out in two-species mixtures (*Pinus sylvestris-Fagus sylvatica*) and the effect of overyielding on productivity stability may increase with increased species diversity. (2) *Species asynchrony* refers to the asynchronous responses of species to temporal variation in environmental conditions and is a consequence of niche differences among species (Loreau and de

Mazancourt 2008). Therefore, well-designed mixed plantations including species with contrasting climatic preferences may stabilize productivity by lowering (σ) (Loreau and de Mazancourt 2013). Species asynchrony can be thought of as a form of temporal complementarity among species and has been shown to be a key driver of stability both in grasslands (Hector et al. 2010; Hautier et al. 2014) and in forests (del Río et al. 2014, 2017; Jucker et al. 2014), in accordance with the insurance hypothesis (Yachi and Loreau 1999). (3) *Species interactions* such as facilitation or reduced competition among neighbouring trees may allow mixed-species communities to reduce interannual variation in productivity increasing the efficiency with which the resources are used (del Río et al. 2014; Forrester 2014). In addition, the higher temporal stability in mixed stands may be linked to interannual shifts in species interactions (del Río et al. 2017). Therefore, the temporal variation in niche complementarity between species may be a key factor to explain the increase in temporal stability (del Río et al. 2017).

Given that tree mixtures may stabilize productivity over time better than monocultures, the establishment of mixed plantations can improve plantations' resilience in terms of productivity in the face of climate change, which is expected to increase the frequency and intensity of disturbances and stress events.

9.5 Mixed Carbon Plantations to Cope with Global Warming

Lately, reforestation and recovery of degraded lands are recognized as mechanisms to help meet emission reduction targets and to deal with global warming. Currently, global deforestation is the second largest source of carbon emissions after fossil fuel combustion (Le Quéré et al. 2015). Recently, both governments and the private sector are increasingly using tree plantations to offset carbon emissions (Hulvey et al. 2013). REDD+ is an example of climate mitigation mechanisms through incentivizing land managers to reduce carbon emissions from deforestation and degradation and to enhance forest carbon stocks (Parrotta et al. 2012; Pawson et al. 2013).

Nevertheless, it has been observed that many carbon offset projects use monocultures with exotic fast-growing trees to try to maximize carbon sequestration (Chazdon 2008; Hunt 2008; Diaz et al. 2011). This, as we have seen, may have consequences on the resistance and resilience capacities of plantations for facing the many different risks and uncertainties in long term. A recent meta-analysis indicates that mixtures sequester at least as much aboveground carbon as the most productive monocultures in any given location (Hulvey et al. 2013). The results suggest that increasing tree diversity in carbon plantings, particularly adding species that facilitate stand-specific growth (e.g. nitrogen fixer species), may increase carbon storage.

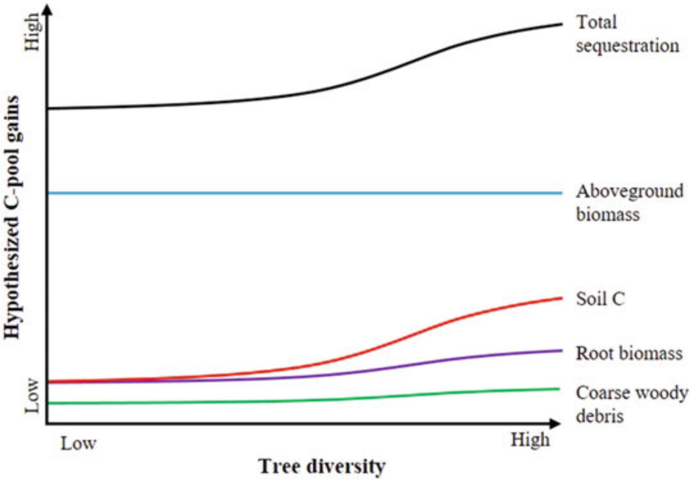

Fig. 9.2 Illustration of a hypothetical long-term C sequestration in each C pool and the summed of all the C pools along a tree diversity gradient (Adapted from Hulvey et al. 2013). By increasing the tree diversity along with select species that contribute to the formation of different C pools (coloured lines), it maximized the total C sequestered (black line)

Furthermore, early results from TreeDivNet indicate that the performance of high carbon sequestering species might be contingent upon the diversity of the community (Verheyen et al. 2015). For example, it was observed that *Alnus glutinosa* and *Betula pendula* were more efficient at storing carbon in mixtures than in monoculture.

However, the carbon sequestration capacity of a stand is not limited to storage through aboveground biomass but also roots, soil and coarse woody debris that may store significant amounts (Fahey et al. 2010). Moreover, the development of the different C pools depends not just on richness but also species identity (Diaz et al. 2009). That is, a species which contributes the most to the development of a C pool, such as aboveground biomass, may not play the same role in the formation of another, such as root biomass (Diaz et al. 2009). That is why well-designed plantations which include increased tree diversity, as well as key species that contribute to the formation of different C pools, may be more efficient than monocultures at storing C (Hulvey et al. 2013) (Fig. 9.2).

A forest plantation that has carbon sequestration as one of its objectives must be planned to store the carbon sequestered into the future. As noted before, mixed-tree plantations may be more resistant, resilient to different disturbance events as well as more stable in biomass production. Moreover, mixed plantations may adapt better to slow, directional change such as gradual warming or atmospheric nitrogen related to climate change, thus providing better conditions for long-term carbon sequestration under environmental changes.

9.6 Conclusion

Developing a novel long-term forest management under future ecological and social uncertainties and risks is a challenge that must be addressed under the premise of increasing diversity. Mixed plantations dilute the impact of disturbance agents due to the different sensitivities and recovery mechanisms of species to specific disturbances. Therefore, the resistance against disturbance is increased, and recovery post-disturbance is facilitated. In this chapter, we have shown how mixed plantations may better cope with ecological and social disturbances than monocultures. While it is true the currently available evidence does not support that mixed plantations are always more resistant to ecological disturbances when compared to monocultures (e.g. drought), choosing compatible tree species for mixtures will assist in achieving the desired mixing effects (selection effect) through management. In addition, mixed plantation also may reduce variation in growth over time and stabilize productivity more efficiently compared to monospecific stands. Ultimately, a planting approach that includes increased species diversity as well as key species that contribute to the formation of a variety of C pools may help to achieve a higher C storage and other ecosystem service goals.

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Chapter 10
Models for Mixed Forests

Marek Fabrika, Hans Pretzsch, and Felipe Bravo

Abstract The basic classification of models based upon the modelling concept distinguishes empirical, process-based and structural models. Universal multidimensional classification distinguishes ten model categories practically very important. Character of input data for forest models depends mainly on the concept of the model and its category. Different tools for input data can be utilised. Extensive set of components, which deal with different parts of forest development, is also available. They are, e.g. partial models addressing mortality, competition, growth, nutrient cycle, thinning interventions, felling approaches or regeneration establishment. The output data also depends primarily on the concept of the model and its category. Generally four essential principles can be applied for modelling of mixed stands as follows: (I) weighted mean of pure stand characteristics, (II) considering mixing effects by multipliers, (III) spatially explicit competition model, (IV) ecophysiological process approach. Different levels of model applicability for simulating mixed forest stands exist. Suitability level for mixed stands increases from the top downwards, and it is joined with model categories and essential principles used.

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10.1 Classification and Categories of Forest Models

Current research provides a wide selection of models, which vary not only in their principles and algorithms but also in the software design. The basic classification of models based upon the modelling concept (Kurth 1994) distinguishes empirical, process-based and structural models. **Empirical models** (i) use statistical relationships derived from empirical data gathered at research, monitoring or inventory plots. **Process-based models** (ii) are based on known causal relationships within ecophysiological and ecosystem processes (e.g. radiation absorption, pedotransfer functions, water balance, transpiration, stomatal conductance, leaf energy balance, photosynthesis, respiration, allocation, senescence, etc.). **Structural models** (iii) deal with the development of tree morphology on the base of tree architecture and topology of organs, e.g. using the elements of fractal geometry, recursive L-systems and vector graphics.

In addition to this basic classification, different approaches exist that classify models according to their temporal-spatial hierarchical level (Pretzsch 2001), object-spatial hierarchical level (Lischke 2001) or other classifications by Munro (1974), Shugart (1984), Vanclay (1994), Liu and Ashton (1998), Houllier (1995), Franc et al. (2000), Porte and Bartelink (2002) or Pretzsch (2009). The description of the character of individual categories can be found in monographs dealing with forest modelling, e.g. Pretzsch (2009), Weiskittel et al. (2011), Burkhart and Tomé (2012) or Fabrika and Pretzsch (2013). For this study we chose the classification according to Lischke (2001), which was modified by Fabrika and Pretzsch (2013) and subsequently simplified to its final form (Fig. 10.1). The presented classification can be considered as universal because of its multidimensional nature. It accounts for the modelling object (i), spatial resolution (ii), temporal resolution (iii), and applied concept (iv). Model type depends upon the level of a modelled object (organ, organism, class/cohort, population or ecosystem) and spatial resolution (object coordinates in 3D space, horizontal position of an object in 2D space, or membership of an object to a bio-group, stand or a region). Level of modelled object describes main (principal, elementary) object which is defined by state variables changed during simulations. Change of object's state is influenced by exogenous or intermediary variables describing environmental conditions. Environmental conditions can be changed in different spatial resolution. The level of a modelled object is shown in the columns of the classification described with the letters of Greek alphabet, and the spatial level is given in the rows of the classification marked with Roman numerals. The level of an object is also correlated to temporal resolution of a model, which is shown on the time axis in front of the classification matrix. The intersection points of the object and spatial levels represent the model category. The categories are shown in Fig. 10.1 by the position in the matrix. The colour of model mark indicates the prevailing modelling concept: process-based (grey), structural (white) or empirical (black). The categories are marked with Arabic numerals. The following models are practically very important and should be addressed:

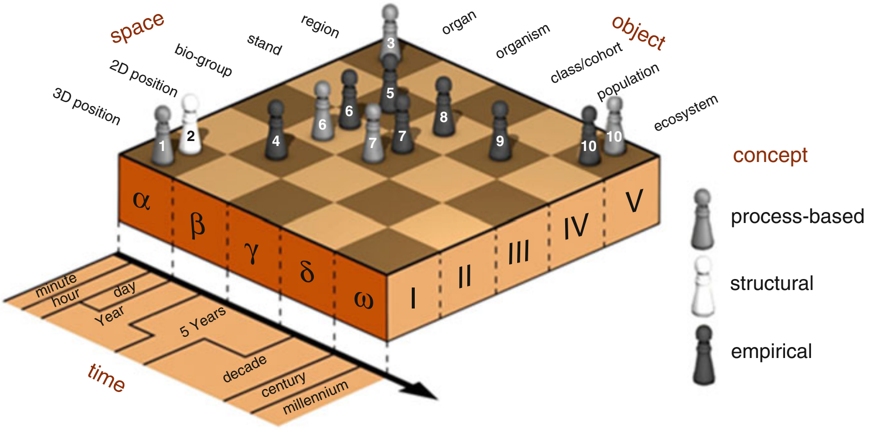

Fig. 10.1 Classification of models according to object, space, time and concept. So far, the classification has defined 10 categories of models: ecophysiological tree models (1), functional-structural plant models (2), big-leaf models (3), empirical distance-dependent (spatially explicit) tree models (4), empirical distance-independent (spatially non-explicit) tree models (5), tree gap models (6), cohort gap models (7), distribution stand models (8), population (species) stand models (9) and biome models (10). The position of the model category in the matrix classifies a model on the base of a modelling object and spatial resolution. Temporal resolution is correlated to a modelling object. The colour of a model mark defines a dominant concept. Future development may fill other positions of the classification

1. **Ecophysiological tree models** (αI) simulate causal processes (Landsberg and Sands 2011), while their basis is assimilation in foliage of individual trees. Leaves or needles can be modelled with separate objects or more frequently with generalised objects in the form of solids of tree crown or its layers. The position of these objects in 3D space of a stand is important for the level of radiation absorption. Different approaches are applied, e.g. the method of ray tracing (Brunner 1998). The result of the production is net biomass that is allocated (divided) into other tree organs. Pfreundt (1988) was the pioneer of the described modelling principle and the first person who used this principle for forest modelling followed by Hauhs (Hauhs et al. 1995), who presented TRAGIC model. From newer models we can name, e.g. BALANCE model (Grote and Pretzsch 2002, Rötzer et al. 2009).
2. **Functional-structural plant models** (αI) deal with modelling the development of plant morphology in time and space. Their foundations were laid by Prusinkiewicz based on the ideas of Lindenmayer (Prusinkiewicz and Lindenmayer 1990). The principle is based upon growth grammars (morphemes), which define recurring replacement of tree parts with new parts in a recursive manner. In this way, branching structures (graftals) are created and are displayed using vector (turtle) graphics. Hence, they originate in the fractal

geometry and the so-called L-systems. The shape and the size of new plant structures depend on ecophysiological processes, in particular photosynthesis, which are directly built in the growth grammars. As an example we can name GROGRA (Kurth 1999), LIGNUM (Perttunen et al. 1998) or GroIMP (Kniemeyer 2008) products.

3. **Big-leaf models** (αV) generalise the assimilation organs in the form of an abstract leaf, which represents the whole spatial unit of an ecosystem, e.g. 1 m^3. The performance of the assimilation of an abstract leaf is identical to the performance of a modelled ecosystem in a spatial unit. Another assumption is that the spatial unit is homogeneous from the point of its tree crown cover homogeneous and represents a certain type of vegetation. Radiation absorption is solved on the basis of leaf area index of the homogeneous crown cover, e.g. using Lambert-Beer law that is sometimes combined with Campbell method of ellipsoid orientation of assimilation organs (Campbell 1986, 1990). The founders of this principle are models 3-PG (Landsberg and Waring 1997) or Biome-BGC (Thornton 1998).
4. **Empirical distance-dependent (spatially explicit) tree models** (βII) are based on empirical relations between tree increment (diameter and height), environmental conditions (e.g. site index of a stand or a set of site conditions) and competition pressure on a tree. Competition pressure is simulated using competition indices dependent on the position and dimensions of the surrounding trees. The foundations of this approach were laid by FOREST model (Ek and Monserud 1974). From newer models we can mention, e.g. SILVA (Pretzsch et al. 2002, Pretzsch 2009) or SIBYLA (Fabrika 2005) models.
5. **Empirical distance-independent (spatially non-explicit) tree models** (βIV) are of a similar character, but tree positions are not necessary for modelling the competition. The competition pressure is derived using the total area (crown cover or density) or tree position within the cumulative frequency function of the selected biometric characteristic. This simplified approach of modelling competition was introduced in the STAND PROGNOSIS MODEL from Wykoff et al. (1982). From later models we can mention products PROGNAUS (Sterba 1995) or BWIN (Nagel 1996).
6. **Tree gap models** (βIII) divide the area of interest to bio-groups of trees (e.g. 100 to 1000 m^2). They focus on modelling the growth of individual trees in bio-groups. Biometric characteristics of trees (diameter, height) in groups are known. Tree positions are not taken into account, but the position of bio-groups is important because they determine the dynamics of the vegetation (succession) in the modelled region. From the pioneers of this modelling principle we can name Botkin et al. (1972) with JABOWA model, and Shugart and West (1977) with FORET model. From newer products we can mention, e.g. PICUS (Lexer and Hoenninger 2001).
7. **Cohort gap models** (γIII) were created by Bugmann (1994), who proved that the trees that are similar at the beginning of the simulation remain similar during their entire lives. Considering this fact, he divided the trees in bio-groups into

so-called cohorts, which represent generations of trees characterised by distinctive heights. Cohorts are represented by one typical individuals and the number of trees in cohorts. Trees do not change their membership of the cohort. In a cohort, tree number can only be reduced due to mortality. Only the growth of a typical tree of a cohort is simulated, which saves computing time without significant impact on simulation results. Bugmann presented this approach in the model ForClim (Bugmann 1996).

8. **Distribution stand models** (γIV) address frequency dynamics of a selected biometric parameter. For the given characteristic, classes are created, e.g. diameter classes. Temporal forest growth dynamics is simulated on the basis of modelling the frequency change of classes. Classes do not change, only the membership of trees in classes change. This differentiate these models from the previous group, where cohorts acted as classes, the size of which can change, but the membership of trees in cohorts remains constant. In this category of models, an entire forest stand is divided into classes. In the previous category of models, bio-groups of trees are divided into cohorts. The simplest way is changing frequency function during time by modification of parameters (Clutter 1963 and von Gadow 1987). Other possibilities are distribution models based on transition rates between diameter classes. They were first developed over 50 years ago by Lewis (1942) and Usher (1966). This type of model has gained particular popularity for the management of uneven-aged and mixed-species stands. Computer simulation programmes based on matrix models, which are neither individual-based nor process-based (Liang and Picard 2013), have been developed for various kinds of forests (e.g. Liang et al. 2006). Furthermore, Markov decision process models (MDP, e.g. Suzuki 1971 and Sloboda 1976) have been developed to reduce the non-linearity and structural complexity of matrix models for broader-scale applications. However, because matrix models are based on the tree population structure rather than on individual tree competition, structure, and growth, they are not readily applicable for the integration of individual tree-based silvicultural guidelines.
9. **Population (species) stand models** (δIV) represent most traditional models. Their beginnings go back to yield tables (Assmann and Franz 1963, Hamilton and Christie 1973, Vuokila 1966, Schmidt 1971, Lembcke et al. 1975, Halaj et al. 1987). They simulate the development of mean and area stand parameters (e.g. mean diameters, mean heights and growing stocks) on the base of site type. They are derived exclusively from empirical regression models that are frequently based on growth functions. Models have a limited validity (model stand type, model stand density, model regime of forest management). They are bound to represent the entire population or species in a forest stand. More flexible models of this type are models STAOET (Franz 1968) and DFIT (Bruce et al. 1977).
10. **Biome models** (ωV) assume that the composition of vegetation (biomes) changes with environmental conditions (e.g. temperature and precipitation). They deal with changes of climax vegetation types over long time periods (centuries to millennia). The first and nowadays a classical representative is

the model by Holdridge (1947). From newer models we can mention, e.g. BIOME (Prentice et al. 1992) or DOLY (Woodward and Smith 1994).

The above-mentioned 10 categories of models can currently be considered as the basis, from which further possible modifications are derived. The location of the model type in the classifications is marked with their typical placement, and some variations may, however, occur outside their typical position. For example, big-leaf models are usually used at a regional level of vegetation types (Biome-BGC by Thornton 1998, position αV), although they can also be successfully applied at a stand level (Forest-BGC by Running and Gower 1991, position αIV). The same is true for the colour of mark in the classification, which represents modelling concept. In the classification we chose a prevailing concept for a given type of models. However, some variants also use other concepts. For example, the model ANAFORE by Deckmyn et al. (2008) simulates the change of typical individuals in cohorts (modelling object) at a stand level (spatial resolution) using process-based modelling concept. Hence, it is a category γIV, which was originally created for empirical models and static classes and not for process-based models and dynamic cohorts. A similar example is GOTILWA (Gracia et al. 1999) model, which belongs to the same category as ANAFORE model, but instead cohorts, GOTILWA uses the original principle of dividing populations into permanent diameter classes. This model also uses the principle of modelling the development of a typical individual in diameter classes with a process-based concept.

The current trend is to perform **hybridisation** of models. Hybrid models combine several categories of models. They are mutually complementary, i.e. their algorithms are mutually bound. Another trend is to use **downscale** or **upscale** procedures, which enable shifts from a more general modelling level to a more detailed level (downscale) or vice versa from a more detailed level on a more general level (upscale) using a serial approach. The second procedure is more frequent in the literature (see works by King 1991, Rastetter et al. 1992, Bugmann et al. 2000, Dieckmann et al. 2000, Auger and Lett 2003, Urban 2005, Lischke et al. 2006). In addition, a parallel approach of a **multiscaling** type can also be applied, when one product uses several types of mutually unbound models in parallel, which are selected depending on the purpose of simulations, as it is, e.g. in the current version of SIBYLA (http://sibyla.tuzvo.sk).

The model classification is not only versatile, but also open. This means that, if in science or practice, the need for a new category of models is identified, a new position of a given colour mark can be put on a particular square of the classification. A similar principle has been applied for the current development of forest models. For example, the first position (δIV) was filled with yield tables, and so far the last position (αI) was occupied with ecophysiological tree models and functional-structural plant models.

10.2 Input Data for Forest Models

Character of input data for forest models depends mainly on the concept of the model and its category. The **concept** of the model affects the overall nature of input data. Empirical models require biometric parameters of trees or stands or a generalised site description (based on site classification or a set of other indicators of resource supply and environmental factors) as input. Process-based models require inputs that are directly linked to ecophysiological and ecosystem processes. First of all, they include climatic and soil characteristics with fine resolution (hours, days). State variables of an ecosystem, which directly affect the intensity of processes, are also needed. For example, photosynthesis is determined by leaf area and respiration by the size of initial biomass. Structural models require mainly the description of the initial tree morphology using growth grammars or other methods to determine tree architecture and topology of their organs.

The **category** of the model also affects the character of input data. In particular, it specifies the type of the modelled object and thus the detail of input data. Different data sets are required for different levels: the level of an ecosystem or population, the level of cohorts or classes and the level of an organism or even organs. For example, at a population level species composition, stand density and tree species parameters (mean diameter, mean height, basal area or volume) are important, while at a level of an organism tree diameter, tree height, crown parameters and, in the case of distance-dependent models, also positions of trees in the plot are important. This also holds for empirical models. For process-based models, another data set is required. For example, for a population leaf area index and total biomass per species are important, while at a level of organisms, leaf area of a single tree, biomass of individual tree parts and its spatial distribution (2D or 3D) are important.

As the modelling detail increases, the set of input data also increases. Considering temporal, economic, methodological and technological limits for the acquisition of input data, models often comprise auxiliary tools, which derive more detailed input from commonly available or more general data. This saves time and costs even if it is at the expense of output accuracy. As an example we can name various interfaces for forest inventories, tools for structure reconstruction and reproduction, structure generators, site generators, weather generators or models for the numerical weather prediction.

Interface bound to **forest inventory outputs** contains various computer procedures and algorithms, which can provide or derive necessary data from available inventory databases or geographic information layers.

Tools for **structure reconstruction** are connected to special methods of field data collection, such as field GIS sets (Černý and Bukša 2005), terrestrial laser scanning (Simonse et al. 2003, Aschoff et al. 2004, Heurich et al. 2004, Hopkinson et al. 2004, Pfeifer et al. 2004, Bienert a Scheller 2008, Klemmt and Tauber 2008) or remote sensing methods, e.g. aerial photogrammetry (Gougeon 1995, Dralle and Rudemo 1997, Brandtberg 1999, 2002, Gitelson et al. 2002, Surový et al. 2004), aerial laser scanning (Magnussen and Boudewyn 1998, Harding et al. 2001, Persson et al. 2002, Popescu et al. 2002, Heurich et al. 2003, Lim et al. 2003, Blaschke et al. 2004, Clark et al. 2004, Holmgren and Persson 2004), etc. The aim of these procedures is to derive (reconstruct) parameters of objects from obtained data layers or survey materials, e.g. to derive the position of trees or their biometric parameters (diameter, height, crown parameters), or for some types of models to reconstruct the morphology of stems or tree crowns.

Forest **structure generators** were developed for the purpose of generating more detailed data from more general data, e.g. to generate tree diameters, tree heights, crown parameters and position of trees from the information about mean diameter, mean height and volume or stand basal area. For structure generation, the methodologically proved approaches (Nagel and Biging 1995, Merganič and Sterba 2006), which ensure that the values of more general input data remain the same, are used. At the same time, they create a structure, which by its nature suitably represents the modelled stand. Some algorithms even account for the pattern and proportion of the species mixture (Pretzsch 1997).

Tools for forest **structure reproduction** represent a specific category derived from the tools used for structure reconstruction and structure generators, since they are used to generate an unknown forest structure outside inventory plots on the basis of the known structure at inventory plots (Pommerening 1999, Pommerening et al. 2000). It means that a part of trees represents a real situation (inventory plots) and a part is filled in by structure generators. Reproduction is used to create so-called representative stands.

Site generators are used to derive the data on site conditions, which are not available from usual information sources. They are used in models that require average or aggregate climatic characteristics as input for modelling the intensity of growth processes. An example of such situations is modelling of tree increments (effect) on the base of the value of a site variable (dose) and cumulating of effects caused by multiple site variables (Kahn 1994). Site generators derive required variables on the base of the commonly available data, e.g. geographical coordinates or forest region, elevation, aspect and slope of the terrain, etc. Different approaches are used, e.g. climate regionalisation using geoinformatic procedures (Fabrika et al. 2005).

Weather generators are used primarily in process-based models that require information on weather characteristics for short time periods, e.g. hours or days. Due to the frequent unavailability of such data, they are generated using models, which the average or aggregate meteorological data representing a longer period, usually a year or a growing season, distribute to individual months, days and hours. Algorithms usually use statistical approaches. At present there are many models of this nature. As examples of such models, we can name WGEN (Richardson and Wright 1984), SIMMETEO (Geng et al. 1986, 1988), TAMSIM (McCaskill 1990), CLIMGEN (Clemence 1997), MET&ROLL (Dubrovský 1997), LARS-WG (Semenov et al. 1998), AAFC-WG (Hayhoe 2000), MARKSIM (Jones and Thornton 2000), RUNEOLE (Adelard et al. 2000), WM2 (Hansen and Mavromatis 2001) or CLIMA (Donatelli et al. 2009).

Models of numerical weather prediction are used everywhere, where scenarios of temporal development of climatic characteristics are required for simulations of future forest production. They are mostly models of atmospheric physics that use quantitative methods for simulating interactions between atmosphere, oceans, earth's surface and ice. Models are very complex and demanding for computing power. Therefore, supercomputers or other technologies of high-performance computer processing of data are frequently used. In Europe, a well-known and frequently used model is ALADIN (Huth et al. 2003).

Some of the above-mentioned tools for collecting input data are universal and can be used in all categories of models, e.g. the interface to forest inventories. Others are specifically tied only to some model types. For example, tools for forest structure reconstruction are applicable everywhere, where the information about tree parameters and tree positions and eventually also about their morphological structure is required. In such a case, the initial condition reproduces the real state. Structure generators can also be applied in those tree models, for which the information about tree position is not required, or generated tree positions that do not necessarily copy the real state are sufficient. Tools for structure reproduction combine both approaches. They provide tree models with tree positions, of which a part are real tree positions and a part are generated positions. Site generators can be used in all types of models, except for the models that require site specification only on the base of a site index derived from stand characteristics (e.g. height site index). In the models that require weather data with a time resolution of an hour, day or a month as input, weather generators can be implemented. Models for the numerical weather prediction can be applied in all models that are able to respond to change in climatic characteristics. The applicability of the auxiliary modules in individual model categories is shown in Table 10.1.

For the applications in mixed stands, the models that account for the horizontal and vertical stand structure are more suitable because they enable capturing mutual interaction of trees due to their mixing within a stand. This implies that tools for structure reconstruction, reproduction and generation are particularly useful.

10.3 Components of Forest Models

Since nowadays there exist a great number of model categories, an extensive set of components, which deal with different parts of forest development is also available. They are, e.g. partial models addressing mortality, competition, growth, nutrient cycle, thinning interventions, felling approaches or regeneration establishment. The applicability of these components for modelling mixed forests depends not only on the nature of the model itself, but also on the forest stands character and the purpose of forest simulation. The following Tables 10.2, 10.3, 10.4, 10.5 and 10.6 present a list of available components and of the methods used including the indication of their suitability for each category of models.

Table 10.1 Tools for importing input data into forest models. They are suitable for different categories of the models and some of them are useful for application in mixed forests

Tool for input data	Model category									
	Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Forest inventory interfaces	+	+	+	+	+	+	+	+	+	+
Structure reconstruction tools	+	+	–	+	–	+	–	–	–	–
Structure generators	+	+	–	+	+	+	–	–	–	–
Structure reproduction tools	+	+	–	+	–	+	–	–	–	–
Site generators	+	+	+	+	+	+	+	–	–	–
Weather generators	+	–	+	–	–	+/–	+/–	+/–	–	–
Numerical weather prediction models	+	+	+	+/–	+/–	+/–	+/–	+/–	–	+/–

Note: + ... tool is suitable for the category of models, - ... tool is useless for the category of models

Table 10.2 Components for modelling tree mortality

Category of component	Component	Methods	Model category									
			Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Mortality sub-models	Intrinsic mortality	Constant probability method	+	+	+	+	+	+	+	–	–	–
		Stand density rule by Reineke	+	+	–	+	+	+	–	–	–	–
		Self-thinning rule by Yoda	+	+	+	+	+	+	+	–	–	–
		Maximum basal area by Assmann	+	+	–	+	+	+	–	–	+	–
		Frequency function	–	–	–	–	–	–	–	+	–	–
		Yield function	–	–	–	–	–	–	–	–	+	–
	Growth dependent mortality	Logit model	+	+	–	+	+	+	–	–	–	–
		Discriminant function	+	+	–	+	+	+	–	–	–	–
		Threshold method	+	+	–	+	–	–	–	–	–	–
		Classification and regression tree	+	+	–	+	+	+	–	–	–	–

(continued)

Table 10.2 (continued)

Category of component	Component	Methods	Model category									
			Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
	Exogenous mortality	Monte Carlo risk method	+	+	+	+	+	+	+	+	+	–
		Fuzzy rules method	+	+	–	+	+	+	–	–	–	–
		Logit method	+	+	–	+	+	+	–	–	–	–
		Classification and regression tree	+	+	–	+	+	+	–	–	–	–
		Chaos theory	–	–	–	–	–	–	–	+	+	–

Note: + ... tool is suitable for the category of models, - ... tool is useless for the category of models

Table 10.3 Components for modelling tree competition

			Model category									
Category of component	Component	Methods	Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Competition sub-models	Calculator of competition indices	Crown intersection by Bell	+	+	–	+	–	–	–	–	–	–
		Hegyi's method	+	+	–	+	–	–	–	–	–	–
		Sum of circular segments by Alemdag	+	+	–	+	–	–	–	–	–	–
		Ratio of tree dimensions according to Martin and Ek	+	+	–	+	–	–	–	–	–	–
		Horizontal cross-section method	+	+	–	+	+	+	–	–	–	–
		Crown competition factor	+	+	–	+	+	+	–	–	–	–
		Ratio of tree crown sizes by Biging and Dobbertin	+	+	–	+	–	–	–	–	–	–
		Competition for crown light by Pretzsch	+	+	–	+	–	–	–	–	–	–

(continued)

Table 10.3 (continued)

Category of component	Component	Methods	Model category									
			Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
	Space analysis tool	Area rasterisation/ Voxelisation	+	+	–	+	–	–	–	–	–	–
		Delaunay triangulation	+	+	–	+	–	–	–	–	–	–
		Spatial distances method	+	+	–	+	–	–	–	–	–	–
		Hemispherical projection method	+	+	–	+	–	–	–	–	–	–
		Ray tracing method	+	+	–	+	–	–	–	–	–	–
		Lambert-Beer method	+	+	+	–	–	–	–	–	–	–

Note: + ... tool is suitable for the category of models, – ... tool is useless for the category of models

Table 10.4 Components for modelling tree growth

Category of component	Component	Methods	Model category									
			Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Growth sub-models	Empirical algorithms	Regression method	–	–	–	+	+	+	+	+	+	+
		Multiplication method	–	–	–	+	+	+	+	–	+	–
		Reduction of growth potential	–	–	–	+	+	+	+	–	–	–
	Modelling of photosynthesis	Proportional method	+	+	+	–	–	+	+	–	–	+
		Empirical sensitivity to environmental conditions	+	+	+	–	–	+	+	–	–	+
		Michaelis-Menten kinetics method	+	+	+	–	–	+	+	–	–	+
		Method according to Farquhar and von Caemmerer	+	+	+	–	–	+	+	–	–	+
	Modelling of morphological development	Lindenmayer systems	–	+	–	–	–	–	–	–	–	–

Note: + ... tool is suitable for the category of models, – ... tool is useless for the category of models

Table 10.5 Components for modelling nutrient cycle

Category of component	Component	Method or element	Model category Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Nutrient cycle sub-models	Pedotransfer functions	Modelling soil hydrological limits	+	+	+	–	–	+	+	–	–	+
		Modelling soil properties	+	+	+	–	–	+	+	–	–	+
		Modelling soil nutrients	+	+	+	–	–	+	+	–	–	+
	Hydrological balance	Interception	+	+	+	–	–	+	+	–	–	+
		Evaporation	+	+	+	–	–	+	+	–	–	+
		Transpiration	+	+	+	–	–	+	+	–	–	+
		Run-off and drainage	+	+	+	–	–	+	+	–	–	+
	Stomatal conductance	Jarvis method	+	+	+	–	–	+	+	–	–	+
		Ball and Berry method	+	+	+	–	–	+	+	–	–	+
	Leaf energy balance	Iterative methods	+	+	+	–	–	+	+	–	–	+
	Respiration	McCree method	+	+	+	–	–	+	+	–	–	+
		Thornley method	+	+	+	–	–	+	+	–	–	+

	Allocation	Empirical method	+	+	+	–	–	+	+	–	–	+
		Allometric method	+	+	+	–	–	+	+	–	–	+
		Teleonomic balance method	+	+	+	–	–	+	+	–	–	+
		Metabolic pool method	+	+	+	–	–	+	+	–	–	+
		Proportional source-sink method	+	+	+	–	–	+	+	–	–	+
		Resistance to transport method	+	+	+	–	–	+	+	–	–	+
		Mechanical constraints method	+	+	+	–	–	+	+	–	–	+
		Pipe model	+	+	+	–	–	+	+	–	–	+

Note: + ... tool is suitable for the category of models, - ... tool is useless for the category of models

Table 10.6 Other supporting components of forest models

Category of component	Component	Method or element	Model category									
			Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Other supporting components	Thinning model	Method of biosociological position	+	+	–	+	+	+	+	+	–	–
		Future crop trees methods	+	+	–	+	–	–	–	–	–	–
		Target dimensions methods	+	+	–	+	+	+	+	+	–	–
		Equilibrium curve methods	+	+	–	+	+	+	+	+	–	–
		Removal function methods	+	+	–	+	+	+	+	+	–	–
		Thinning line methods	+	+	–	+	+	+	+	+	–	–
		Thinning indices methods	+	+	–	+	+	+	+	+	–	–
		Geometric methods	+	+	–	+	–	–	–	–	–	–
		Interactive methods	+	+	–	+	–	–	–	–	–	–

	Regeneration felling model	Clear-cutting elements methods	+	+	−	+	−	−	−	−	−	−
		Shelterwood methods	+	+	−	+	−	−	−	−	−	−
	Regeneration establishment model	Natural regeneration	+	+	−	+	+	+	+	−	−	−
		Ingrowth	+	+	−	+	+	+	+	−	−	−
		Artificial reforestation	+	+	−	+	+	−	−	−	−	−

Note: + ... tool is suitable for the category of models, − ... tool is useless for the category of models

Following the work of Keane et al. (2001), forest **mortality** can be divided into intrinsic, growth-dependent and exogenous mortality. Intrinsic mortality represents the number of trees that die due to the limits in the production space. Considering the research performed so far, the following methods are available: a method of constant probability (Botkin 1993, Bugmann 1996), Reineke rule of stand density (Reineke 1933), Yoda self-differentiation rule (Yoda et al. 1963), maximum basal area according to Assmann (Assmann 1961), frequency functions (Sloboda 1976, von Gadow 1987) or yield functions (Halaj et al. 1987, Petráš et al. 1990). Growth-dependent mortality characterises the number of trees that die due to the conditions in the stand and competition pressure of the neighbouring trees. Currently, the following methods are available: logit model (Vanclay 1995, Ďurský 1997, Tang et al. 1997, Monserud and Sterba 1999, Palahí et al. 2003, Bigler et al. 2006), discriminant function (Wyckoff and Clark 2000), method of threshold competition pressure (Nagel 1996, Pretzsch 2009) or classification and regression trees (Fan et al. 2006). Exogenous mortality is the result of external factors, which cause unexpected disturbances. According to the literature overview, this type of mortality has been successfully addressed through risk modelling (hazard, exposure and vulnerability) using approaches based on Monte Carlo principles (Fabrika and Vaculčiak 2009), the method of fuzzy rules (Fabrika and Vaculčiak 2009), logit model (Hasenauer 1994), classification and regression trees (Baker 1993) or chaos theory (Pavlík 2009).

Competition between trees is most frequently addressed by calculating competition indices or by spatial analysis. The following competition indices are known from the literature: crown intersection by Bell (1971), method according to Hegyi (1974), sum of circular segments by Allemdag (1978), ratio of tree dimensions according to Martin and Ek (1984), horizontal cross-section method (Wensel et al. 1987), crown competition factor (Sterba 1989), ratio of tree crown sizes (Biging and Dobbertin 1992), competition for crown light by Pretzsch (1995) etc. Their overview can be found in Bachmann (1998). The models that require a more detailed spatial description use more complex tools to analyse the space. Different approaches are used, e.g. space rasterisation (Faber 1983, Nagel 1985) or voxelisation (Greene 1989), Delaunay triangulation (Jack 1968, Fraser 1977, Pelz 1978), method of spatial distances (Pretzsch 1992), method of hemispherical projections (Biber 1996), method of ray tracing (Brunner 1998, Fabrika and Merganič 2010), application of Lambert-Beer law (Monsi and Saeki 1953), etc.

Modelling **tree growth** uses various methods that are in particular related to modelling concept. From available empirical approaches, we can name regression methods (Franz 1968, Petráš et al. 1990, Sterba 1995), multiplication methods (Kangas 1968, Wenk 1972, Fabrika 1998), methods of growth potential reduction (Hasenauer 1994, Nagel 1996, Pretzsch et al. 2002), etc. The description of the methods can be found in Fabrika and Pretzsch (2013). The process-based concept of forest modelling is based on the quantification of photosynthesis. For this purpose, the following methods are now available: proportional methods (Kellomäki and

Strandman 1995, Deluze and Houllier 1997, Mäkelä 1997, Reffye et al. 1997), methods of empirical sensitivity to environmental conditions (Weinstein et al. 1991), method of Michaelis-Menten kinetics (Monsi and Saeki 1953), method of Farquhar and von Caemmerer (1982), etc. Their description can be found in Landsberg and Sands (2011). From approaches of the structural concept, algorithms based on Lindenmayer systems (Prusinkiewicz and Lindenmayer 1990) are most frequently used.

A specific group of modelling approaches is modelling a nutrient cycle. This group of methods is related to the process-based concept of modelling forest growth. Modelling of pedotransfer functions nowadays includes modelling of soil hydrological limits (Saxton 2009), modelling of soil properties (McKenzie and Cresswell 2002, Saxton and Rawls 2006), modelling of soil nutrients, etc. Within the frame of hydrological balance, the following processes can nowadays be algorithmically solved: interception (Aston 1979, Jiagang 1988, Anzhi et al. 2005), evaporation (Ritchie 1972, Choudhury and Monteith 1988, Zhang et al. 1996), transpiration (Monteith and Unsworth 1990), water run-off and drainage (Almeida et al. 2007), etc. Stomatal conductance can be solved using the approaches of Jarvis (1976), Ball and Berry (Ball et al. 1987) or other algorithms. Leaf energy balance is modelled using various iterative algorithms based on thermal balance or other approximation methods. Process of respiration can be quantified using the equations of McCree (1970), Thornley (1970), etc. For modelling biomass allocation, many methods are available, e.g. empirical methods (Rauscher et al. 1990, Zhang et al. 1994), allometric methods (Mäkelä and Sievänen 1992, Deleuze and Houllier 1995), methods of teleonomic balance (Davidson 1969), metabolic pool method (Bassow et al. 1990, Baumgärtner et al. 1990, Harpaz et al. 1990, Weinstein et al. 1991, Wermelinger et al. 1991, Grossmann and DeJong 1994, Hoffmann 1995, Thaler and Pagès 1998), proportional source-sink method (Warren-Wilson 1972), resistance to transport method (Thornley 1972), method of mechanical constraints (McMahon and Kronauer 1976, Cannell and Dewar 1994), pipe model (Shinozaki et al. 1964), etc.

From other important components for forest models, it is necessary to mention thinning models, felling models and regeneration models. Currently available **thinning models** are methods based on biosociological position of trees (thinning from above or from below, Kahn 1995, Ledermann 2002), method of future crop trees (Albert 2001, Eckmüllner 2002), method of target dimensions, equilibrium curve method (Liocurt 1898, Meyer 1952), removal function method (Kennel 1972, von Gadow 1987), thinning line method (Nagel 1996), method of thinning indices (Halaj 1976), geometric methods, interactive methods (Seifert 1998, Fabrika 2003), etc. They are described in Fabrika and Ďurský (2005) and Fabrika and Pretzsch (2013). Models of **regeneration felling** are aimed at extracting trees from a mature stand. They are designed as systems based on clear-cutting regeneration elements or on the methods of shelterwood management. They use suitably modified thinning models, e.g. regeneration elements are solved using geometric thinning, or the elements of shelterwood management are based on the method of target dimensions or methods based on biosociological tree position. To extend the forecasts for a period longer than one generation of a stand, various algorithms for modelling natural regeneration, ingrowth or planting named as models **of regeneration establishment** are used. An overview of some methods can be found in Price et al. (2001).

10.4 Output Data from Forest Models

The output data depends primarily on the concept of the model and its category. Generally the set of primary output state variables of the model is similar to a set of input state variables into the model. Empirical models are focused on biometric variables of modelled objects (trees or stands), process-based models are focused on net primary production of objects (leaves, branches, stems, roots), and structural models are concentrated on the morphology of objects (topology of a stem and branches). Apart from the primary state variables, models also produce derived outputs, for example, empirical models can derive the value of biomass and of the accumulated carbon from primary biometric variables, or from the net primary production produced by process-based models, biometric parameters can be calculated using, e.g. carbon allocation to individual tree compartments (stem, branches, roots, etc.). Furthermore, many models scale up the simulation results from the organ or organism level to the stand level (unit area of 1 ha). In addition to common production outputs, it is also possible to calculate, derive or estimate other outputs, e.g. the assessment of forest structure, forest biodiversity, calculation of costs and benefits, and an estimate of forest ecosystem services, etc. Of special interest for forest management is the provision of information on timber quality (Pretzsch and Rais 2016) and the link to simulation of saw timber (Poschenrieder et al. 2016). For climate change research, output variables such as groundwater provision or C-storage (Rötzer et al. 2009, Rötzer et al. 2010) might be of primary interest.

Most models provide outputs in the form of data tables usually coupled with some type of a database, spreadsheet, text or XML file. Some models also enable data visualisation in a form of comprehensible charts. Considering the complexity of forest structure, forest visualisation is also used. For this purpose, different methods can be considered: horizontal projection, vertical profiles, 3D projection, rendered scenes or a virtual forest. Visualisation can be used in those categories of models, which are based on defining the position of objects in 2D or 3D space, while the modelling and information unit is an individual tree, or its organs. Rendered scenes are primarily used in functional-structural models, for which morphological tree parameters are also known. Other types of visualisation are suitable also for the remaining subset of models (Table 10.7). A very efficient way of forest visualisation is a form of virtual reality, which allows a user to move inside the virtual forest or to interact with trees (marking, felling), which shifts forest modelling towards trainers (Seifert 1998, Fabrika 2003). The description of the methods of forest visualisation can be found in Fabrika and Pretzsch (2013).

Table 10.7 Character of output data from forest models

		Model category									
Data character	Methods	Ecophysiological tree models	Functional-structural plant models	Big-leaf model	Distance-dependent empirical tree models	Distance-independent empirical tree models	Tree gap models	Cohort gap models	Distribution stand models	Population (species) stand models	Biome models
Production of data tables		+	+	+	+	+	+	+	+	+	+
Production of charts		+	+	+	+	+	+	+	+	+	+
Forest visualisation	Horizontal projection	+	+	–	+	–	+	–	–	–	–
	Vertical profiles	+	+	–	+	–	+	–	–	–	–
	3D projections	+	+	–	+	–	+	–	–	–	–
	Rendered scenes	–	+	–	–	–	–	–	–	–	–
	Virtual forest	+	+	–	+	–	+	–	–	–	–

Note: + ... tool is suitable for the category of models, - ... tool is useless for the category of models

10.5 Level of Applicability of Forest Models for Mixed Stands

The prognosis of mixed forest development is a much more complex scientific issue than the prognosis of pure stands. The problem lies in the need to reflect interspecific interactions, which result from their different demands on environmental conditions and mutual filling of stand space, which is often more structured than in pure stands. Even-aged mixed stands may also create vertically more structured forests due to different growth rates of individual tree species. Due to this, mixed forests are in general able to use stand space (both horizontal and vertical) better than pure stands. Pretzsch (2009) showed that the development of basal area in mixed stands depending on stand density significantly deviates from the Assmann theory of basal area in pure stands (Assmann 1961). He also showed that incremental interactions also depend on the proportion of mixed tree species (Pretzsch et al. 2010, 2013).

Generally four essential principles can be applied for modelling of mixed stands as follows:

I. Weighted Mean of Pure Stand Characteristics

The prediction of the stand growth of mixtures commonly follows one of the four main algorithms introduced in the following (Table 10.8). If no information is available, mixed-species stand dynamics is simply predicted as the weighted mean of the pure stands' productivity. Firstly, appropriate pure stand models (e.g. yield tables or diameter distribution models) are chosen for the respective species. Secondly, sub-models for the respective site index and thinning are chosen. Thirdly, the species-specific time series of growth and yield characteristics (e.g. productivities) are read out of the pure stand models and used to calculate the weighted mean based on the mixing proportions. In this way, mixing proportions (m_1, $m_2 \ldots m_n$) in the mixtures are used for calculating their expected performance as a weighted mean of

Table 10.8 Four common principles for predicting the growth of mixed-species stands and their main pros and cons

Principle	Pros	Cons
I. Weighted mean of pure stand characteristics	No knowledge of mixed stands required, easy to apply, first guess	Emergent properties of mixed stands ignored, overyielding neglected
II. Considering mixing effects by multipliers	Statistical knowledge of mixing effects exploited, easy to integrate into models	Dependency of mixing effects of site conditions and type of mixing ignored
III. Spatially explicit competition model	Interactions between growth and structure considered, light competition integrated	Unspecific consideration of environmental conditions on mixing effects
IV. Ecophysiological process approach	Integration of system knowledge, extrapolation of dynamic behaviour	Many patterns and processes hardly understood, model validation still poor

According to Pretzsch et al. (2015)

the pure stand productivity (e.g. $p = p_1 \times m_1 + p_2 \times m_2 + \cdots + p_n \times m_n$). Other stand growth characteristics such as tree number, basal area, standing volume or basal area growth are derived analogously. This method considers no interactions between the mixed species, which might modify their long-term development. Mixed-species stands' dynamics is deduced from yield tables representing the species' behaviour in monospecific stands. The yield tables for monospecific forest stands by Assmann and Franz (1965) and Schwappach (1889), and the yield tables for mixed stands of Norway spruce and European beech by Wiedemann (1942) are common examples of this concept.

II. Considering Mixing Effects by Multipliers

In case that the deviation of stand growth and stand density of mixed-species stands from the corresponding monospecifc stands is known, the mixing effects may be integrated using multipliers. In this way growth and yield characteristics at the stand level (e.g. mean tree, stand density, current annual stem volume growth) or at the individual tree level (e.g. tree diameter, crown size, tree diameter increment) which are well known for monocultures can be adjusted. Thus the species' behaviour in an interspecific environment can be taken into consideration. Multipliers may be derived from long-term experimental plots or forest inventories by comparing mixed-species stands with neighbouring monocultures. The modifier approach is common for modelling the effects of site conditions, insect disturbances, or fertilising effects statistically, even when the underlying mechanisms are not yet understood (Wykoff et al. 1982; Komarov et al. 2003, Monserud and Sterba 1996).

III. Spatially Explicit Competition Model

A third approach represents individual tree models which abstract forest stands by their vertical layering or three-dimensional structure using the tree height, height to crown base, crown width, tree coordinates, etc. In empirical models, the 2D or 3D structure is the basis for calculating competition indices for every tree as a proxy for the availability of growing space and resources. The resulting competition indices are used to regulate the tree's growth and probability of survival in the subsequent period. Based on the estimates of individual growth rates and survival/dropout, the size of all trees and the structure of the whole stand can be simulated. Stand growth and species-specific growth is then calculated by integrating the growth and considering the mortality of all individual trees. The updated stand structure is the basis for the next simulation cycle with time steps of commonly 1 or 5 years. Due to the feedback loop between stand structure and tree growth via the competition indices, mixing can significantly affect stand development. For instance, species-specific space occupation in different layers of the canopy, increasing stand density compared with pure stands or reducing or even out-competing one of the species can be considered. In these empirical tree-level models, the species' competition for resources is modelled by their competition for space, and the type of resource (water, light, nutrients) is not specified. When individual tree models of this type are parameterised using data from monospecific stands, the directly integrated mixing effect is mainly the species-specific growing area requirement and the response to competition. If such models are parameterised using data from mixtures, various effects of competition and facilitation might be indirectly represented in the estimated parameters. Model examples for this approach are the models by Hasenauer (1994), Köhler and Huth (1998), Pretzsch et al. (2002, 2007) and Pukkala et al. (2009).

IV. Ecophysiological Process Approach
Process-based models are different from empirical models mainly by considering the actual resource and environmental factors for regulating growth and mortality rather than using competition indices. The competition for resources is simulated for each individual tree or cohort. Consequently, the influence of species mixing is realised by feedbacks between species-specific spatial structures and tree growth. In addition it is represented by the feedback between a tree's individual environment in terms of the within-stand resource supply, and its growth and mortality. Light distribution within the stand or for an individual tree and the uptake and consumption of water and nutrients all depend on species mixing and determine the growth of trees, cohorts and entire stands. Model example for these concepts represent the works by Grote and Pretzsch (2002), Kellomäki and Vaisanen (1997), Kimmins et al. (1990a and b, 1999) and Rötzer et al. (2009).

Fig. 10.2 describes levels of model applicability for simulating mixed forest stands. The figure includes two main levels: (**a**) proportional mixing of models developed for pure stands and (**b**) application of models developed for mixed stands. Level B is then divided to levels B1–B5 which increase suitability for mixed stands in this order. Each level also includes suitable model categories and applied essential principles.

Despite the acknowledged causalities, predicting the development of mixed stands can be addressed using models of pure stands. In this case it is performed on the base of the assumption that tree species composition is constant during the whole simulation. The simulation is carried out separately for each tree species using the models of pure stands, and the mixed stand development is predicted as the weighted mean of the respective monospecific stands. This approach can be applied using big-leaf models (Fig. 10.1, category 3), distribution stand models (Fig. 10.1, category 8) and population (species) stand models (Fig. 10.1, category 9). Regarding essential approaches the models can utilise both principles: weighted mean of pure stand characteristics (I) or in addition considering mixing effects by multipliers (II). Approach (II) is more appropriate, but since the assumption of constant tree species composition during forest stand development may be speculative, this approach is recommended only if models of mixed stands are not available.

However, the use of models developed for mixed stands does not guarantee the correspondence with the real development of a forest stand. The success of the prognosis is related to the fact how exactly the interspecies interactions of tree species resulting from their different demands and mutual filling of stand space is captured by the model. The suitability of models for simulating mixed stands increases from the models that do not account for spatial structure, through the

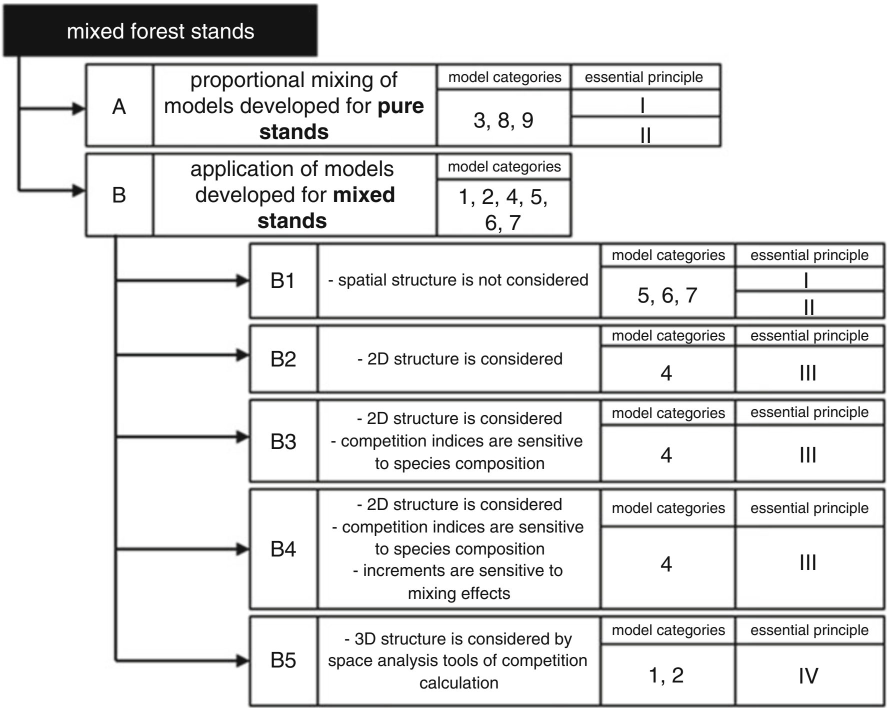

Fig. 10.2 Levels of model applicability for simulating mixed forest stands. Suitability level for mixed stands increases from the top downwards

models which consider horizontal (2D) structure, up to the model which take a comprehensive spatial structure (3D) into account. The level of model application is indicated in Fig. 10.2. From models, which do not recognise the spatial structure, the following models are available: empirical distance-independent (spatially non-explicit) tree models (Fig. 10.1, category 5), tree gap models (Fig. 10.1, category 6) and cohort gap models (Fig. 10.1, category 7). The models usually implement essential principles (I) and (II). If the mixing effects are considered by multipliers (principle II), the models are more suitable for mixed stands. Among the models, which capture horizontal tree distribution and therefore also distribution of tree species, are empirical distance-dependent (spatially explicit) tree models (Fig. 10.1, category 4). In this category of models, mutual interaction between tree species is ensured by competition indices, which account for spatial distribution and dimension of surrounding trees. Their suitability is increasing, if competition indices are also sensitive to species composition. As an example we can name competition indices with modification coefficients that depend on the species or a group of species the partial competitor belongs to. Particularly suitable indices are those, which are based on the accumulation of the competitive pressure of individual competitors in the tree surrounding, mainly the indices based on the method of a vertical light cone (Pukkala and Koloström 1987, Pukkala 1989, Biging and Dobbertin 1992, Pretzsch 1995). Even more significant improvement can be achieved when the interactions between different tree species are accounted for tree increment values, as it was presented by Biber et al. (2013) in SILVA model. Mixing effect is included in the form of a multiplier, which modifies the value of tree increment depending on the index of tree growth potential and the percentage of species mixed in the stand. All model types which consider horizontal structure (2D structure) belong to essential principle (III).

From the methodological point of view, the best way of modelling the development of mixed stands is to account for the complex 3D space (horizontal and vertical). Especially suitable models for these purposes are ecophysiological tree models (Fig. 10.1, category 1) and functional-structural plant models (Fig. 10.1, category 2). Their suitability depends on the position of individual trees in the stand space and on the level of consideration of resource utilisation based on advanced spatial analysis methods, e.g. space rasterisation (Faber 1983, Nagel 1985), space voxelisation (Greene 1989), Delaunay triangulation (Jack 1968, Fraser 1977, Pelz 1978), method of spatial distances (Pretzsch 1992), method of hemispherical projections (Biber 1996), method of ray tracing (Brunner 1998, Fabrika and Merganič 2010), application of Lambert-Beer law (Monsi and Saeki 1953), etc. Regarding essential principles for predicting the growth of mixed-species stands, the models belong to the most suitable principle (IV): ecophysiological process approach. While in mainly light-limited systems, this detailed modelling of the structure and process in the canopy space can contribute essentially to predicting the mixing effects, under water and mineral nutrient limitation the focus may be rather on the below ground processes.

10.6 Concluding Remarks

Due to different modelling concepts, model categories, input and output data as well as implemented model components, when using the mixed forest model, it is important to proceed as follows:

(a) Consider the purpose of modelling.
(b) Take account of existing input data and the necessary output data.
(c) Select the appropriate model category (Fig. 10.1) that matches the target modelling detail (object, space, time).
(d) For a larger set of available models, prefer those that are more suitable for mixed forests (Fig. 10.2, bottom-up selection).
(e) Use, as far as possible, the methods of evaluation, validation and adaptation, e.g. calibration of models (Fabrika and Pretzsch 2013, page 152), on a set of empirical data that originates from the territory for which we want to apply the

model but was not used to construct the model itself (the principle of independent validation).

(f) Always interpret simulation results based on the character of the model and its limits.

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Chapter 11
Optimizing the Management of European Mixed Forests

Lauri Valsta and Jette Bredahl Jacobsen

Abstract Mixed forests have a potential of providing a wider set of ecosystem services compared to single-species forests. Economic analyses on mixed forests should be based on values of service offerings and on dynamical interactions between different tree species over time. The benefits can be realized when managerial decisions utilize the potential of mixed forests. This requires flexibility in species composition and stocking over time. The multiple ecosystem services provided by mixed forests call for more advanced valuation methods, such as joint production optimization and monetizing the ecosystem services. Case studies are reviewed that solve these problems in different contexts.

11.1 Introduction

Ecological properties and effects of mixed forests have been addressed in different sections of the present volume (Bravo 2018; Preztsch 2018; del Río et al. 2018). This chapter concentrates on the economic aspects of managing mixed forests as such and as alternatives to single-species forests. The emphasis is at stand-level mixtures. Forest areas with several different single-species stands provide some of the benefits but fail to acknowledge the utilization of ecological niches and interactions between tree species and those among other flora, fauna, fungi and microbes.

Given the goal to maintain and increase mixtures in European forests, economic analysis helps in identifying superior combinations of species and in demonstrating the incentives for forestry decision makers to enhance mixtures. The incentives may

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be for forest owners' economic benefits or policy makers' tools for advancing policy goals. The applied policy measures depend on the structure of forest ownership in each country because the mechanisms to influence decision making are largely different between managers of public forests and private forest owners. However, for example, informational instruments can be applied to both ownership cases, and these instruments are directly based on research knowledge.

As forest ecosystems provide services over long time periods, the time factor becomes an important element. This is further emphasized by the long payback periods involved in forest management investments and the long-term effects of forest harvests. While it is expected that forest owners appraise the benefits from forest based on a positive discount rate, it is not immediately evident that the society should apply positive discount rates. However, to maintain many ecosystem services, there is currently an urgency to achieve, for example, biodiversity values or climate change mitigation effects. With a zero discount rate, the society would imply a valuation that it can wait an indefinite time for the ecosystem service offerings. This would not be acceptable as the value of natural capital (of the ecosystems) could be severely compromised by a negligent attitude.

The benefits from a forest area are always accrued from the various forest ecosystems present. Hence, mixed forests can also be viewed as elements in a portfolio, similar to an investment portfolio. Then, the risk-return behaviour becomes important, and it can be analysed with portfolio methods.

11.2 Framework of Analysis

As any forests, mixed forests are connected to multiple benefits and costs. Some of them are valued on markets and are, as such, directly measurable. Currently many of them are not, but that does not make them less important. However, without valuation they may be more difficult to address in decision making.

All valuations are context dependent. Perhaps the most important context element is the stakeholder. Typical stakeholders in forestry are the private forest owner, the public or corporative forest owner or planner and the general public. A common perception of the stakeholder in European forestry has been the forest owner (private or large scale) facing the markets for forest production outputs and inputs (see, e.g. Hiley 1930, Johnston et al. 1967, Speidel 1967, Bright 2001). The economic valuations pertaining to the stakeholder are largely shared across those that consider the market valuations as relevant. This works out well for traditional timber management. However, non-market valuations may be much more distinct across stakeholders.

The studies described in this chapter share the common view that the stakeholder is a forest owner or planner who bases forest management decisions on market prices of tangible products and various valuations of intangible products or services of the forest. For the latter, the ecosystem service concept (MEA 2003) is often applied to include the different products and services that forests provide for the individual or the society. In some studies, the stream over time of ecosystem service offerings is interpreted as the value of natural capital (Daly 1994). Inversely, the natural capital is thought to provide a rent value, which is the annual provision of ecosystem service.

What makes mixed forests different in service provision from single-species forests are the dynamic effects that different species have on each other and on the rest of the elements of the ecosystem. Some studies imply that different species in a mixed forest merely co-exist and do not affect each other anymore than individuals of the same species. For example, Hynynen et al. (2011) report that mixtures of Scots pine and silver birch yielded merely according to a linear combination of the species stockings.

Several individual studies have reported that mixtures provide a higher yield than a plain combination of the yields of species (e.g. Mielikäinen 1980, 1985, Huber et al. 2014, Toïgo et al. 2015 Pretzsch and Biber 2016, Preztsch 2018). Also, the meta-analysis by Piotto (2008) reports a higher yield of mixtures. Usually, the studies have reported yields from more or less fixed species proportions over the rotation or a growth period. Studies with flexible species proportions will be reported below.

11.3 Common Methods

11.3.1 Variations of the Mixture Effect

For forest management decision making, it is useful to define the concept of *mixture effect*. The concept helps in describing the influence that one or more mixing tree species have on a forest stand, compared to a single-species stand. Further, due to the alternatives of analysis, it is necessary to define a few variations of the *mixture effect*. The viewpoint may be observational, as in 3.1.1 and 3.1.2, or managerial, as in 3.1.3 and 3.1.4.

11.3.1.1 Biological-Physical Mixture Effect

We group under this concept the numerous effects that one or more mixing species have on the forest ecosystem compared to a single-species stand. These include enhanced net primary production, yield of biomass or roundwood and provision of other ecosystem services.

11.3.1.2 Economic Mixture Effect

In the economic mixture effect, the provision of products and services identified in 3.1.1 is valued according to their economic value – market value or non-market economic value. Due to different valuations, a biological-physical mixture effect may not necessarily translate directly to an economic mixture effect.

11.3.1.3 Static Management Decision

By defining a mixture management static or dynamic, we refer to the kind of decision making behind the management or nonmanagement of a mixed-species stand. While all forest stands develop dynamically every year, all the ecosystem components interacting in this group decisions about the species composition are made only once for a given time period or the whole rotation. For example, a stand can be established by planting and subsequent vegetation control to a given species composition with the purpose that the composition will prevail approximately at the same level for the period of interest. Subsequent management may also maintain the desired species composition by controlling intermediate harvests. The key point is that the species composition is not deliberately altered over time.

11.3.1.4 Dynamic Management Decision

The dynamic management decision is applied by adjusting species composition over time in order to utilize relative superiorities of different species over the rotation of the forest. The design of species composition may be based on previous knowledge of the successional behaviour of different species, relative to each other, or it may be based on an optimization process producing a superior species composition over time. Here, the composition is adjusted by silvicultural measures, such as vegetation

Table 11.1 Sample studies concerning mixed forests classified according to the type of mixture effect and management decisions

Type of effect	3.1.3 Static management decision	3.1.4 Dynamic management decision
3.1.1 Biological mixture effect	Mielikäinen (1980), (1985), Comeau et al. (2005), Hou et al. (2016), Hynynen et al. (2011), Pretzsch and Biber (2016)	Mielikäinen (1980), (1985), Valsta (1986), (1988) Pukkala et al. (1998)
3(.1.2) Economic mixture effect	Valkonen and Valsta (2001)	Valsta (1986), (1988)
		Carlsson (1992)
		Pukkala et al. (1998)
		Lu and Gong (2005)
		Knoke and Seifert (2008)
		Pukkala and Kellomäki (2012)
		Roessiger et al. (2013)
		Rämö and Tahvonen (2015)
		Matthies and Valsta (2016)
		Miina et al. (2016)

control and thinnings, while also utilizing the relative growth rates of different species.

Table 11.1 lists some studies according to the classification above. The selected studies are mostly European and from the boreal and the temperate zone. Results from a selection of studies are reviewed in the remainder of this chapter.

11.3.2 Valuation Considerations

Applying rotation forestry and computing the net returns from timber production in mixed forests follow that of single-species forests. The standard method is the net present value over an infinite time horizon, the soil expectation value (SEV, Faustmann 1849). The infinite time horizon is necessary because otherwise the different rotation lengths will not be valued properly.

For continuous cover forestry, one cannot repeat identical growth cycles to provide the infinite time horizon, except if a steady-state condition already prevails. The standard method is to extend computations far enough into the future (e.g. 300 years) so that the monetary value of items after the horizon becomes sufficiently close to zero because of a positive interest rate (see, e.g. Tahvonen 2011).

The interest on mixed forests is often based on their ability to provide wider ecosystem service offerings than single-species stands. The ecosystem service benefits can be addressed by two principal approaches: constraints analysis or joint production analysis. Constraints are used by first determining the optimum timber production value and, in a stepwise manner, increasing the achievement of another objective (another ecosystem service) and recording the decreases in timber production value. This approach forms a trade-off curve that can be presented to the decision maker.

As an example, consider a two-species, mixed stand of silver birch and spruce. Due to silvicultural practices, there is a scarcity of birch trees in the forest, and an increase in birch provides biodiversity benefits. Two outputs of forest management are compared in Fig. 11.1, providing a trade-off curve. The present value of timber-based returns from the two species is given in the vertical axis and the proportion of birch in stand volume in the horizontal axis. The trade-off curve demonstrates the change in monetary returns due to a change in species composition.

The joint production analysis is based on monetizing the non-timber ecosystem services and maximizing the discounted sum of ecosystem service values. With this method, one makes an inherent assumption that we can set an equal time preference on all ecosystem services (Miina et al. 2010, Matthies and Valsta (2016). However, if other ecosystem services are valued based on grant or subsidy schemes, no contradictions in discounting take place as the services then produce normal monetary returns to the forest owner/decision maker.

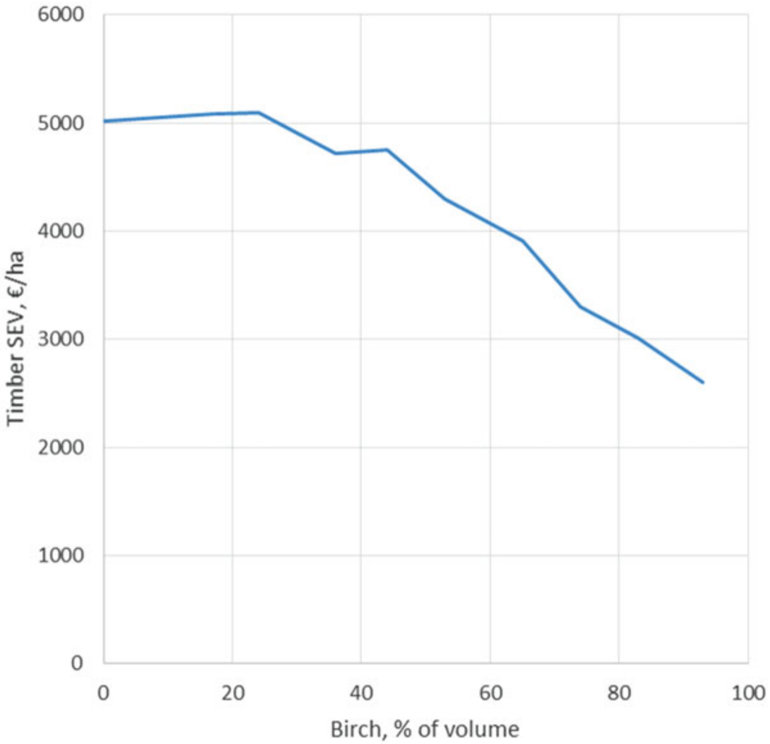

Fig. 11.1 Trade-off curve between monetary returns and share of birch in a Norway spruce-silver birch stand. (Adapted from Matthies and Valsta 2016)

11.3.3 Portfolio Approaches

One reason often raised as an advantage in mixed forests is the diversification of risk due to the inclusion of several species. This diversification may be in terms of biological risks (e.g. pests where not all species are equally prone to certain risks) or in terms of market-related risks. While some studies analyse the effect of a single risk on mixed forests (e.g. Schou 2012), others approach it by analysing variation in return regardless of the origin of the risk (Knoke and Wurm 2006). It is worth noticing that unless an interaction effect occurs by having species mixed in a single stand, the diversification benefit does not differ depending on whether species are mixed at a stand level or a forest level – as the output that is relevant is for an entire management unit. But for small-scale forest owners, it may, of course, be an issue.

Identifying optimal portfolios is challenging in practice for several reasons. First, quantification of the risk is needed, and if we are looking at multiple sources of risk, that may be problematic. This is the example if we want to use it for forecasting. Second, because of the long-time horizon in forestry, conditions change over time.

Looking at price uncertainty, for example, even if we are able to characterize the price variation well, the relative value of each species in the portfolio may change over time, leading to different combinations being optimal depending on which point in time we look at. Third, as management decisions are taking over a long time, each single decision plays into a given condition – which can only slowly be changed. So, if a forest manager, for example, finds out that he/she wants more oak in the portfolio to diversify the risk, it will take many years before this is realized. And it may be optimal to let it take a very long time, because if not, he/she may over a 200-year period have a diversified portfolio, but within a shorter time span, say the 50 years during which he intensively converted to oak, it will be very undiversified. Consequently, diversification needs to take both space and time into consideration. Fourth, in many countries in Europe, forest owners have other assets than forests, and the forest is actively used as an investment in a broader portfolio. Consequently, it can be argued that it is not only the risk within the forest that is relevant to consider but also the risk in the forest relatively to other assets. Probably because of these reasons, portfolio management in terms of forestry is often treated as a conceptual thinking rather than leading to an explicit result of an optimal portfolio. While many studies dealing with portfolio management of forestry focus on a single output – timber (e.g. Mills and Hoover 1982; Reeves and Haight 2000; Knoke and Wurm 2006) – more recently, there has been an increased focus on diversification in terms of output too (e.g. Raes et al. 2016). This complicates the design of the optimal portfolio even further.

11.4 Illustrative Case Studies

While ecological and yield studies on European mixed forests have been published for more than a century (Knoke et al. 2005), economic studies have evolved much later. Apart from comparing field experiments with different species compositions, economic analysis of the mixture effect requires a stand growth model with interspecies dynamics. Such a model enables one to create different strategies where species composition is altered over time. When a growth and yield model is combined with an optimization method, flexible economics analyses can be performed.

In fisheries economics, the multispecies problem has been treated rigorously earlier than in forestry, see, for example, the seminal book by Clark (1976). The first studies incorporating a growth and yield model and optimization, known to the author, were Valsta 1986 (for the growth and yield model by Mielikäinen 1980) and Valsta 1988 (for the growth and yield model by Mielikäinen 1985). Thereafter, several studies emerged in the USA (Haight and Monserud 1990; Yoshimoto et al. 1990), Sweden (Carlsson 1990; Lohmander 1992) and Finland (Pukkala et al. 1994, Vettenranta 1996).

11.4.1 Biological Mixture Effect with Static Management Decision

Among the studies in this group, the study by Pretzsch and Biber (2016) is highlighted. It reports an extensive set of research plot triplets, each of which consists of three research plots (one mixed and two pure stands). The plots were of high density (unthinned or only slightly thinned), and the mixtures had prevailed over time. The management decision to enable a mixture had been done at an early age of the plot. Thus, the species proportions were "static", not purposefully adjusted over time. The results indicated that the mixed forest is capable of maintaining a higher stand density, which supports the earlier results on higher yields. Overall, a biological mixture effect was demonstrated.

11.4.2 Biological Mixture Effect with Dynamic Management Decision

The species composition is affected by thinnings over the rotation. This provides opportunities to adjust the species composition over time in order to maximize the yield benefit of a mixture. There may be existing knowledge about the relative growth rates of the species, or an optimization algorithm can be linked to search for the most productive species composition over time.

Valsta (1988) is chosen to illustrate a case where the species composition of a Norway spruce-silver birch mixture is optimized to achieve maximum annual increment over rotation. Starting with 0, 10, 20,..., 90, 100% birch in the initial

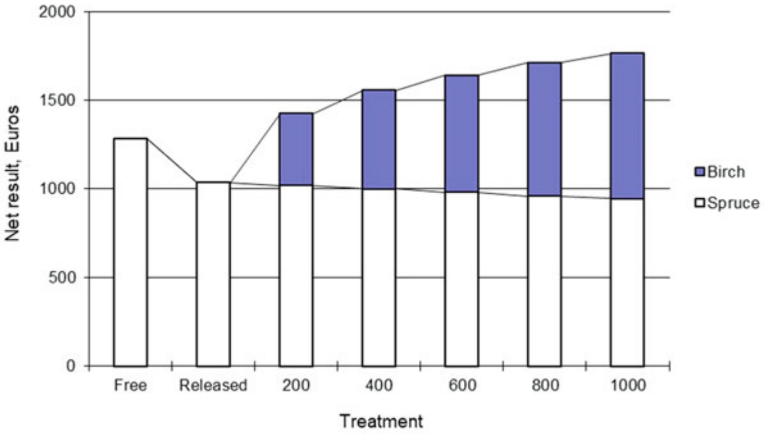

Fig. 11.2 The maximum M.A.I. in relation to species composition of the total volume production during the rotation (Valsta 1988)

stand, the optimization determined the optimum thinning schedule for all initial mixtures in order to maximize M.A.I. or net present value. The result of M.A.I. maximization is given in Fig. 11.2. Because of the dynamics of species interaction, the cumulative birch percentage values changed from the initial values set in 10% intervals. For example, the second leftmost data point has moved to the right. This is because birch had a faster growth at early age compared to spruce.

If there would be no mixture effect, the M.A.I. values would align with a straight line, indicating linear combinations. The area above the straight line depicts the magnitude of the mixture effect at different mixing ratios.

11.4.3 Economic Mixture Effect with Static Management Decision

This group of studies is characterized by a management decision made once during the rotation. The mixture effect can then be described based on different values on the decision variable. The study by Valkonen and Valsta (2001) concerned two-storied mixed stands of Norway spruce (*Picea abies*) and birch species (*B. pendula* or *B. pubescens*). At age 15 of spruce, the birch component of the young stand was thinned to various degrees of density ranging from 200 to 1000 trees per ha. Results for 70-year rotations and 4% real interest rate indicated that the greater the total net present value for Norway spruce and *B. pendula*, the larger the birch component (Fig. 11.3). A similar result but with smaller increments was obtained for *B. pubescens* mixtures.

The study concluded that growing a naturally emerged birch overstory in a spruce plantation up to commercial volume and sawlog size is profitable in Finland with the

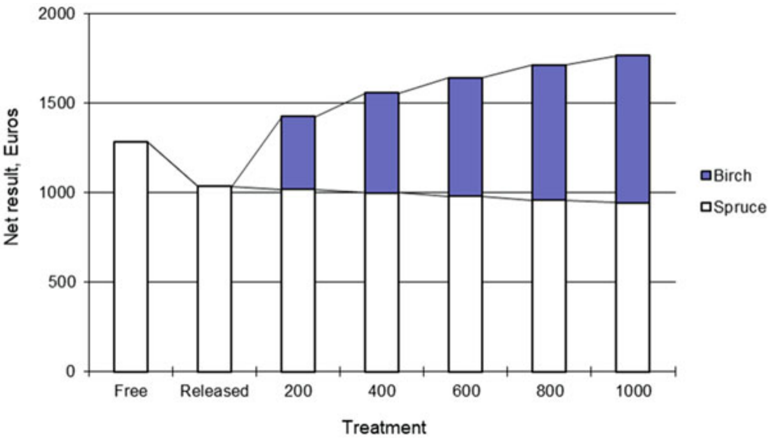

Fig. 11.3 Net present values per hectare (at 4%) for different overstory mixtures of *P. abies* and *B. pendula* (Valkonen and Valsta 2001)

current economic and technical conditions. The most profitable treatment seemed to be to grow 500–800 birch stems per ha up to about 40 years of age for *B. pendula* and 45–50 years for *B. pubescens*. Using *B. pendula* results in significantly higher productivity and net returns than *B. pubescens*. The results were rather insensitive to potential changes in birch prices. A 25% decrease in birch prices relative to spruce prices would not make the simulated overstory alternatives unprofitable, but a 50% decrease would do so for many of the less profitable treatments. High spruce mortality due to logging damage (20.1–26.2% of initial stocking) and the application of expensive labour-intensive logging methods in the thinning and removal operations of the birch overstory were accounted for in the calculations. For the 1000 tree case, spruce suffered a loss of 26%, whereas silver birch provided an additional present value of 64%, giving a total present value increase of 38%.

11.4.4 Economic Mixture Effect with Dynamic Management Decision

Because of the interactions of different tree species, improved yields and economic results can be obtained by carefully utilizing differences in volume increment and wood quality development. Traditional silvicultural expertise (e.g. Kelty et al. 1992) may provide important insights.

Stand-level optimization, as available, provides additional guidance about successful and profitable management. It is especially useful in many situations where the number of possible alternative management schedules is very large and human

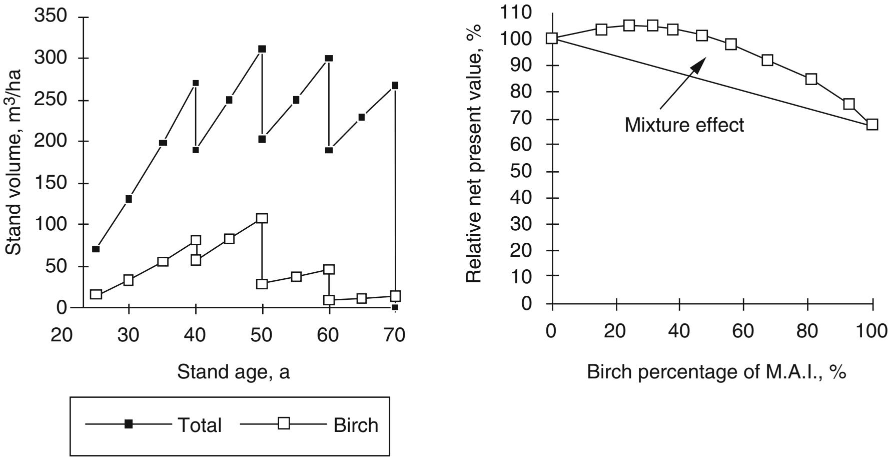

Fig. 11.4 Optimum management of Scots pine-silver birch mixture in Southern Finland (Valsta 1986). The left panel shows the volume development. The right panel shows the present values of different mixtures, determined as averages over the rotation

reasoning has difficulties in accounting for all factors, including densities of different species, the type, intensity, timing and number of thinnings and rotation length. Inclusion of other ecosystem services introduces additional challenges.

For the case of Scots pine (*P. sylvestris*)-silver birch (*B. pendula*) even-aged mixtures in Southern Finland, Valsta (1986) computed the optimum thinning schedule and rotation (Fig. 11.4). The optimum mixture was dominated by pine, and birch had a proportion of 20–40% in the early part of rotation. After the age of 50, birches (the earlier successional species) were gradually thinned away. When optimization was performed for different starting values of birch proportion (at 10% intervals), the corresponding optimal net present values at 3% interest rate were greatest with 20–30% initial birch percentages. A pure pine stand gave a 5% smaller present value than the optimum species composition. Correspondingly, a pure birch stand resulted in a 32% loss. The largest economic mixture effect was 17% (the vertical distance between an optimum and the linear combination of 0% and 100% birch).

Pukkala et al. (1998) analysed Scots pine-Norway spruce mixtures in Eastern Finland using spatial growth and yield models based on temporary sample plots. Stand management was optimized with the net present value over infinite time horizon (soil expectation value), using a 3% real rate of return. The starting point was a mixed stand of 20 years. The optimum solutions for one and two thinning schedules maintained a mixed forest with a decreasing proportion of pine towards the end of the rotation. Thinnings from above were generally optimal for economic objectives of stand management.

Trasobares and Pukkala (2004) studied uneven-aged mixtures of *Pinus sylvestris* and *Pinus nigra* in Northeastern Spain. The diameter increment models included the competing species as a factor, but the basic properties of models were rather similar as well as the ecological niche of the two species. *Pinus sylvestris* dominated in the optimum stand structures, mainly because of its slightly higher growth rates. When *P. nigra* was required to be the dominant tree species, only minor economic losses occurred.

Pukkala and Kellomäki (2012) studied various mixtures of Scots pine, Norway spruce and birch (*B. pendula* and *B. pubescens* combined) in Finland. In economically optimal management regimes, a birch component was utilized at the early stage of the rotation (birches were removed at the second thinning). Towards the end of the rotations, spruce dominance was increased with, typically, 70–75% spruce at final harvest volume. A risk avert decision maker somewhat increased the share of birch, whereas a risk seeker favoured an opposing strategy.

Rämö and Tahvonen (2015) analysed the uneven-aged mixtures Scots pine, Norway spruce and birches (*B. pendula* and *B. pubescens*) for maximum yield and discounted returns. The optimum steady-state structures were characterized by almost pure Norway spruce stands in most cases. On more productive sites, a higher interest rate leads to greater species diversity and a significant birch component. Site productivity, interest rate and relative prices influence the optimum species combination.

In all of the studies reviewed above, a mixture was financially optimal in most cases. A common feature was that one conifer species was the main species, and an admixture of another species was clearly less than 50% but significantly larger than 0%. If the growth model recognized the different growth rhythms of the species with respect to age, the optimal proportions changed over the rotation accordingly.

11.4.5 Multiple Ecosystem Services Analysed

Miina et al. (2016) studied the joint production of timber and wild forest berries, namely, bilberry (*Vaccinium myrtillus*) and cowberry (*V. vitis-idea*). Research was targeted on even-aged stands of Scots pine and mixtures of Scots pine, Norway spruce and silver birch. Market prices of sawlogs, pulpwood and wild berries (paid to berry pickers) were used for optimizing thinnings and rotation in order to maximize the discounted sum of net product values with a 3% discount rate. Stochasticity in berry yields was accounted for.

With average berry prices, the soil expectation value contributions in Norway spruce stands of timber and bilberry were 82% and 18%, respectively, and in Scots pine stands of timber and both berries 53% and 47%, respectively. The berry contributions to revenues are, thus, considerable, subject to the condition that all berries are being picked. The optimum species composition was influenced by the existence of berry yields. For example, if bilberry yields were higher than average, the share of Scots pine would be larger, and rotation length would be increased in optimum management.

Matthies and Valsta (2016) analysed the effect of climate change mitigation on management of mixed Norway spruce-silver birch even-aged stands. The joint production model included timber returns, the value of carbon storage in forests and the radiative forcing effect of forest albedo. Ordinarily, spruce has greater timber returns and carbon storage but lower albedo compared to silver birch. Carbon storage was valued based on emissions offsets, and radiative forcing (based on Kuusinen et al. 2014) was transformed into emissions offsets following Sjølie et al. (2014). Joint production was valued as ecosystem service expectation value (ESEV) covering the three services as discounted values over an infinite time horizon.

The default values for different ecosystem services made a small birch proportion, around 20%, optimal. With increasing emissions offset price, interest rate and albedo difference between the species, the optimum proportion of birch increased. Although the pure spruce stand had the largest carbon storage, the somewhat greater yield of a mixed stand and lower total albedo compensated for carbon storage.

11.5 Discussion and Concluding Remarks

The case studies described above demonstrate that in many cases, a mixture of two or more species is superior in terms of yield and timber economic value or, even more, in joint ecosystem service production. This observation should not be taken as a proof that all mixtures provide greater benefits. One should note that there are studies, for example, Hynynen et al. (2011), where a biological mixture effect was not found. There is, understandably, a possibility of a biased reporting in outcomes in favour of mixtures. However, in most studies the different assumptions and parameter values were varied in order to show the uncertainties of the results.

Studies based on long-term field experiments are often constrained by the more or less static management choices. Model-based studies provide more freedom to identify dynamically changing species compositions that can provide greater benefits than fixed tree species proportions. As the latter studies are based on optimization, they also tend to test the model structures and behaviour and sometimes reveal deficiencies in modelling.

Most of the studies reported here represent the boreal forests of Europe. Studies that utilize growth simulators and optimization algorithms have been somewhat more popular in that region. That may be a result of the simpler stand structures (fewer species and canopy layers) of boreal forests, which may make them more amenable for rigorous optimization.

From timber production point of view, largest benefits seem possible when the mixing species differ in terms of their successional type. This enables forest management to utilize the rapid early growth of one species and sustained growth of a late-successional species within the same rotation. However, these mixtures may be difficult to maintain as the species with rapid early growth may severely weaken the other species during overtopping. The silviculturist would have to manage the stand carefully. A proper spatial arrangement of the competing species seems important. That is also a challenge to research in the field because spatial growth models are not as common as nonspatial models.

Mixed forests are an important component also in uneven-aged forests or continuous cover forestry. Ecosystem services based on structural diversity can be supported by different tree sizes in addition to different species. As the ecological interactions (such as crown competition) at individual tree species level depend both on structure and species, the tree growth models should include spatial information about the size and species of neighbouring trees.

In even-aged stands, especially in planted stands, several studies indicate that location information does not significantly improve the accuracy of stand projection (Busing and Mailly 2004), although also other results exist (e.g. Pukkala 1989). This is to be expected because in stands with repeated thinnings, trees are rather evenly located in the stand and shading is limited. In the contrary, in uneven-aged stands, young trees emerge at locations between existing trees, and the smaller trees are partially shaded by neighbouring larger trees during much of their time. Hence, the competition is spatially characterized and location information improves prediction accuracy.

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Chapter 12
Mixed Forests' Future

Andrés Bravo-Oviedo, Hans Pretzsch, and Miren del Río

Abstract The future of forestry faces the increasing demand of multiple ecosystem services, while coping with biotic and abiotic threatens affecting forest ecosystems. Tree species mixtures as well as structural diversity in monocultures are held to achieve multiple forest services and products while keeping high the options for mitigation and adaption. However, the species- and site-specific dependencies of mixed forest performance do prevent us from considering them as the *panacea* for future generations of foresters who will continue to deal with increasing uncertainties due to changing environment conditions and socioeconomic demands. Here, we summarized the main findings and take-home messages recently compiled in mixed forest research conducted in the context of the European Network on Mixed Forests (EuMIXFOR) with the intention to shed light over the mixed forests' future.

12.1 Introduction

The increment in forest and other wooded land in Europe in the last decade has been accompanied by a recovery in employment in forestry and forest-based industry after the 2008 financial crisis (Eurostat 2017). However, the relative contribution of forestry to the European welfare is still low representing less than 1% in terms of

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GDP in 2010 although this value would be much higher if other forest-related functions and services, e.g., forest-based tourism or wood energy, would be included (FOREST EUROPE 2015). In this context the bio-economy strategy is seen as an opportunity to foster the forestry sector, but it is also accompanied by concerns about its effects on biodiversity (Hall et al. 2012) which is already threaten by environmental and land-use changes. The concerns about the loss of biodiversity and the negative consequences for resilience have suggested adopting strategies toward alternative management regimes (Puettmann et al. 2015), close-to-nature silviculture (Bauhus et al. 2013), climate-smart forestry (Nabuurs et al. 2015), or species-rich forest management options (Bravo-Oviedo 2018) as a response to changes in social attitudes toward forests, their products, and services.

The future of forestry faces the increasing demand of multiple ecosystem services, while coping with biotic and abiotic threatens affecting forest ecosystems. Strategic orientations to protect forests and enhance ecosystem services include protection of genetic resources including tree species diversity and diversity within species and within populations by promoting sustainable forest management as a way of protecting biodiversity (European Commission 2013). This orientation of EU policy is supported by the fact that around one-fifth of the total forest area in Europe comprises a mixture of broadleaves and conifers, and when species are considered individually, 70% of European forests are dominated by two or more species. An example of the increasing interest of multiple species stands is that, in Europe, the sharing of single-species forest is decreasing at an annual rate of 0.6% in a steady form since 1990 while forest land is increasing and so does mixed forests (FOREST EUROPE 2015).

Enhancing and promoting mixtures of tree species might well serve to meet the above mentioned goals as long as the interplay between environmental drivers and site and species response is correctly understood taking into account multiple social demands from forests.

This was the initial motivation to build an European network on mixed forests (EuMIXFOR) aiming to contribute to the increase of knowledge, the sustainability of management, and the future expansion, conservation, and improvement of mixed forests on the basis of science, innovation, and rural development. The specific goals of EuMIXFOR were (1) understanding the role that mixed forests can play in the provision of ecosystem services, (2) addressing how mixed forests can face environmental challenges, (3) identifying silvicultural practices and decision tools to sustainably managing mixed forests, and (4) facilitating the share of knowledge gained from research on mixed forests. This advancement of scientific knowledge on the performance of species-rich forest ecosystems is helping to meet sustainable and biodiversity goals while, at the same time, adopting resilient and adaptive management of mixed forests.

The interest on mixed forests can be traced back in the roots of forestry (Cotta 1828, Hartig 1791, Möller 1922), but it is in the last 20 years when this interest has been boosted (Kelty et al. 1992; Olsthoorn et al. 1999; Pretzsch et al. 2017) in the context of threats associated with global change. Here, we present the contribution of EuMIXFOR in the form of take-home messages to the advancement of knowledge on mixed forest dynamics, silviculture, and management of mixed forests.

12.2 Insights into Dynamics, Silviculture, and Management of Mixed Forests

The below take-home messages about dynamics, silviculture, and management of mixed forests are intentionally grouped and biased toward results and topics discussed by EuMIXFOR community, and they constitute the main findings of the COST Action FP1206 between 2013 and 2017. Nevertheless, other studies are also highlighted and put into context to better summarize EuMIXFOR conclusions.

12.2.1 Research Methods

12.2.1.1 Data Platforms and Demonstration Facilities

Research on forest dynamics needs large periods of time to get confident cause-effect analyses. Long-term experimental settings and observational studies are valuable tools that in the case of mixed forests, dynamics are still scarce (Ruiz-Peinado et al. 2018). The design of mixed forest plantation and experimental designs for research are usually based on the addition or substitution of species (Vandermeer 1989; Kelty and Cameron 1995), i.e., additive or replacement designs, which are essentially plot for comparisons of two species. More complex designs including spacing effects are multispecies Nelder wheels or Goelz's triangle (Goelz 2001; Vanclay 2006). Experimental plantations that manipulate species composition and density to disentangle the biodiversity-ecosystem function relationship have been established across the globe (Verheyen et al. 2016), and observational platforms have also contributed to this aim (Baeten et al. 2013). In the case of species interactions and performance of mixed versus pure stands, the triplet approach is based on the comparison of species growing in pure and mixed plots where within triplet environmental factors are homogenous and between triplet site features may vary. This observational layout allows both isolate true mixing effects and compare their variation across abiotic gradients. Triplet-gradient analyses have proved its validity to test species interactions, and it is considered a fundamental research facility in the long run. In the context of EuMIXFOR, a triplet-gradient facility has been established in *Pinus sylvestris-Fagus sylvatica* mixture (Heym et al. 2017) where studies have been developed about productivity (Pretzsch et al. 2015) and its temporal stability (del Rio et al. 2017), structural diversity (Pretzsch et al. 2016), light interception (Forrester et al. 2017a), crown development (Barbeito et al. 2017), or soil fertility (Błońska et al. 2018), among others.

Research facilities for testing forest management options or final and partial harvests are even scarcer. Some classic experimental designs have been used to test the effect of thinning on radial growth of mixtures (Aldea et al. 2017) or litter decomposition (Bravo-Oviedo et al. 2017), but a similar approach to triplet-gradient would be required to determine true mixing effects.

Research requires demonstration and result outreach to better understand the demand of ecosystem services from society and to transfer outcomes. Martelloscopes are large plots where trees are marked and positioned, and stakeholders are requested to select trees according to different harvest schemes. This demonstration tool helps in understanding the human behavior and professional skills to adopt new silvicultural schemes (Pommerening et al. 2015; Vítková et al. 2016) that in the case of mixed stands might be relevant. Forest inventory also has a potential to reveal the effect of tree species mixing on productivity (Liang et al. 2016) and stand structure (Condés et al. 2017).

12.2.1.2 Species Proportion

True mixing effects might be masked by the species proportion if such proportion is not based on stand area or growing space of the species. If the species proportion by area is not taken into account, it is assumed that all species would have the same growing space requirements in a particular site (Sterba et al. 2014). The implications of overlooking the correction by area when defining the species proportion are greater in mixtures where the species show large differences in maximum density (Sterba et al. 2014). The species proportion by area can be also calculated using tree-level information using metrics derived from the area potentially available for each tree, e.g., the leaf area (Dirnberger and Sterba 2014; Dirnberger et al. 2016).

12.2.2 Tree and Stand Dynamics

12.2.2.1 Mixed Forest Productivity and Its Temporal Stability

The dynamics of mixed forests in terms of volume growth and yield has deserved great attention in the last decade with more emphasis on two-species mixtures with contrasting growth patterns. More research is needed in mixtures with more than two species (Pretzsch 2018). Mixtures have shown to be superior in terms of volume productivity (Pretzsch et al. 2015) with large variation of under- and overyielding between mixtures (Pretzsch and Forrester 2017) indicating a strong species-specific effect on the mixing effect. Some species combination increased its capacity for overyielding in harsh conditions (Bielak et al. 2014). Studies analyzing dependencies of mixing effects on age and inter-annual variation of climatic factors are still scarce (Pretzsch 2018). It is highly recommended to perform long-term experimental research or sampling along gradients of environmental conditions (moisture and temperature), ages, or stages of development (reinitiation phase, stem exclusion, old growth) to better capture the dynamics of growth and yield in mixed forests.

Ecosystem stability as a response to perturbations is a key concept in plant communities in spite of the confusion around the term stability itself (Grimm and Wissel 1997; Ives and Carpenter 2007). Stability studies involving tree species are fewer than other plant species because of difficulties in controlling all factors in mature populations including spatial environmental variation. Del Río et al. (2017) analyzed the temporal stability (TS) of basal area increment in mixed and pure *P. sylvestris* and *F. sylvatica* stands taking advantage of the EuMIXFOR transect across Europe. The hypothesized mechanisms behind TS are overyielding, asynchrony, and shifts in species interactions. However, there are contrasting results indicating that TS can be higher or lower at different hierarchical levels (community, population, or species). Del Rio et al. (2017) findings corroborated that at the community level, species mixture showed temporal stability, whereas at the population and species level, the response is neutral or negative. The main mechanism controlling TS in *P. sylvestris-F. sylvatica* community is the temporal niche complementarity of both species. Overyielding might not be a direct driver of productivity stability although can have indirect effects as it is related to species asynchrony. However, overyielding-asynchrony relationship has been found also absent in communities with more tree species richness (Jucker et al. 2014), and it deserves further attention.

12.2.2.2 Intra- and Interspecific Tree Competition

It has been largely suggested that intraspecific competition is more intense than the interspecific one in mixtures (Kelty 1992) due to complementary effects whose temporal and spatial dynamics is affected by differences in resource acquisition or resource use efficiency (Forrester 2014). However, with species belonging to the same phylogenetic group and less apparent complementarity, the reduction of competition for species growing in the mixture has shown to be positive for *P. sylvestris* L. and neutral for *P. pinaster* Ait. (Riofrío et al. 2017a) or depending on the mixture for both as in the case of *P. pinea* L. and *P. halepensis* Mill. mixtures (Cattaneo et al. 2017).

At the stand level, there is a strong species identity and size-related effects in the sign and direction of competitive effects. Del Río et al. (2014) found negative effects for basal area growth of *P. sylvestris* in the presence of *F. sylvatica*, whereas *Quercus robur* growth decreased with increasing proportion of *F. sylvatica* but increased with larger beech individuals present. The mixture of silver fir and beech did not affect the growth of the component species.

12.2.2.3 Maximum Stand Density and Mechanical Stability in Mixed Stands

The identification of the maximum carrying capacity of a stand in terms of crowding is a keystone issue in silviculture, and it allows understanding the mixing effects on self-thinning allometry. It has been suggested that the maximum density is strongly influenced by the amount of foliage that the species can support based on mechanical properties affecting the bending stress resistance (Dean and Baldwin 1996; Ducey and Knapp 2010). The main hypothesis is that species with low specific gravity (SG) needs more individuals, measured as stand density index (SDI), to support the same foliar biomass than species with high specific gravity leading to a decreasing linear SDI-SG relationship. Climate and species-specific stress tolerances modulate this relationship (Ducey et al. 2017; Bravo-Oviedo et al. 2018). The evidence that the specific gravity of wood of trees growing in mixed stands is lower than those growing in pure stands (Zeller et al. 2017) and that mixed stands can harbor a larger number of stems than pure stands (Pretzsch and Biber 2016) might support the SDI-SG hypothesis. However, large vertical stratification in mixtures (Forrester et al. 2017a, b) and larger crowns due to mixing effects (Barbeito et al. 2017) could indicate more foliar biomass in mixed stands increasing the stocking independently of the SDI-SG relationship due to higher canopy space filling (Pretzsch 2014).

The importance of studying wood density in forests is twofold. On one hand, there is a strong relationship between wood density and the drought stress resistance and C storage, whereas on the other hand, the technological properties of wood are dependent on wood density. Pretzsch and Rais (2016) did not find strong evidence of mixing effects on wood density when analyzing scientific literature. However, wood density response to interspecific competition might be dependent on species composition. Zeller et al. (2017) analyzed a set of EuMIXFOR *P. sylvestris-F. sylvatica* triplets and found lower wood density in the mixture for both species, whereas tree width response was species-specific being increased in Scots pine and decreased in European beech. Lower wood density could lead to mechanical instability against perturbations like windstorms or snow accumulation in the crowns. Averaged low wood density in mixtures has been suggested to increase the tree packing density as more individuals are needed to fully occupy the stand (Woodall et al. 2005), whereas Zeller et al. (2017) also accounted for the relationship between wood density and the stand density index (SDI) being strong for European beech and non-existing for Scots pine. The dependency between wood density and stand density in mixed and pure stands should account for differences in the stand structure (species composition, size, and age distribution) and on abiotic factors (gradients of water availability, windstorm frequency).

12.2.2.4 Size Structure in Mixed Stands

The analysis of size structure dynamics is important to link tree and stand-level studies (del Río et al. 2016, Pretzsch and Schütze 2015) and to help elucidating the behavior of mixing effects across scales. Mixed stands show higher structural heterogeneity than the corresponding pure stands in crown complementary species (Pretzsch et al. 2016) even in mixtures made of species with similar light requirements (Riofrío et al. 2017b).

12.2.2.5 Crown Architecture and Complementary Use of Light in Scots Pine-Beech Mixtures

Mixture increased the size of beech crowns both vertically and horizontally (Barbeito et al. 2017; Forrester et al. 2017a). The mixing effect in beech is stronger in more productive sites (Barbeito et al. 2017). Differences in structure between mixed and pure stands lead to differences in light use. Mixtures of Scots pine and European beech increased by 14% on average the light intercepted with a significant mixing effect on the vertical stratification of crowns (Forrester et al. 2017a).

12.2.3 Silviculture

12.2.3.1 Nursing Effects and Natural Regeneration

A great bottleneck for forest management is the establishment of sufficient saplings following harvest or in nutrient-poor sites. Mixtures of pioneer and late successional species, either by planting or by natural regeneration, can improve the growing conditions of saplings due to facilitative effects (Mason 2014) and can be patent in the dominant species in the long term (Mason and Collony 2018). However, the existence of nursing effects during the establishment phase might not be a guarantee of future species coexistence (Mason and Collony 2016).

Natural regeneration in mixed forests increases the chances for adaptation to environmental changes because of a higher pool of genotypes. In the practice of silviculture, the regeneration of some species is favored by the presence of another in the stand, and the resultant new generation of trees matches local site variations (Matthews 1991). Silvicultural systems should guarantee the preservation of such species, especially in the stand initiation and understory reinitiation phases of stand dynamics where the possibility of creating new mixtures is higher (Löf et al. 2018). However, a more intense management is required if less competitive tree species are going to be favored (Mason et al. 2018; Pach et al. 2018).

The common pitfalls for natural regeneration in mixed stands are similar to those in monospecific stands, e.g., sufficient supply of seed, adequate light and water availability, or absence of herbivores. However, preserving the mixture during the regeneration stage in mixed stands is more challenging because of, among other factors, the selective herbivory pressure over the most palatable species (Löf et al. 2018).

12.2.3.2 Mixed Plantations

The increasing evidence that mixtures are more capable to meet multiple management objectives and ecosystem services have been noticed by scientists and practitioners working in restoration programs and planted forests. Although the combination of terms like tree plantation and biodiversity might be considered an oxymoron (Brockerhoff et al. 2008), the reality is that the role of single- and multiple-species planted forests on the delivery of ecosystem services and associated trade-offs, the performance of mixed plantations, and existing knowledge gaps have been intensively studied for decades (Montagnini et al. 1995; Menalled et al. 1998; Kerr 1999; Montagnini 2000; Kelty 2006; Piotto 2008; Paquette and Messier 2010, 2013; Lindenmayer et al. 2015; Verheyen et al. 2016; Bauhus et al. 2017; Coll et al. 2018), and the interest will continue to increase as the land area occupied by plantations is steadily augmenting (FAO 2015).

Some may argue that planted forests are not true forest as they are only a simplify array of trees planted to meet one single objective, presumably only timber, where biodiversity is absent, and they can be considered as “green deserts.” However, planted forests provide a larger portfolio of ecosystem services when previous land uses are degraded or abandoned crop fields (Bremer and Farley 2010). The documented failure of planted forests to increase the delivery of ecosystem services is often caused by ill-design plantation programs that can be overcome if policy measures, like increasing biodiversity, are considered (Baral et al. 2016). Promoting polycultures instead of single-species plantations is one of such measures aimed to conserve biodiversity without impairing timber production (Hartley 2002).

The appropriate design of plantations must consider the species composition which form the more resistant and resilient structure to environmental changes. Mixtures of species and vegetation structures, i.e., leaving intact old remnants of original vegetation in degraded lands, should be informed by scientific evidence of the trade-offs and appropriateness of the future plantation to cope with current and expected risks. For example, if the expected risk associated with climate warming is longer drought periods, mixtures can increase the evapotranspiration rate due to higher soil exploration leading to a negative effect of tree plant diversity (Urgoiti and Paquette 2018). On the contrary if the risk is associated with higher pest outbreak susceptibility, the mixture can reduce the damage by reducing the probability of infection due to associational resistance (Jactel et al. 2017).

12.2.4 Modeling and Forest Management

12.2.4.1 Modeling Mixed-Species Forest Dynamics

Modeling differential growth pattern, allometry, or interactions due to mixture at different spatial and temporal scales as compared with species performance in pure stands, i.e., mixing effects, remains an issue in forestry as few models can simulate mixing effects at multiple processes (Pretzsch et al. 2015). However, there exist several model alternatives that can be applied to model mixed forest performance as long as the mixing effects are included in the model structure in the form of modifiers or inter- and intraspecific differential competition factors (Pretzsch et al. 2015). Many of the models developed so far act at the population level (single-species stands), whereas mixed stands scale up to the community level. Summing the performance of individual species does not result in the performance of the community (mixed stand) indicating that the mixing effect might be treated as an emergent property.

Emergent property is any ecosystem feature exhibiting different components or performance at a higher hierarchical level and that it cannot be linearly reduced to a lower level (Reuter and Breckling 1999) or that cannot be explained studying individual components due to interactions (Messier et al. 2013). Some examples of emergent properties in forest ecosystems include the stand structure which is related to individual tree features (Parrott and Lange 2013) and stand-level mortality and associated self-thinning trajectory which is related to tree mortality but difficult to upscale (Monserud et al. 2005).

There are four modeling strategies to model mixed forest dynamics (Fabrika et al. 2018): the weighted mean of corresponding pure stands in case of lack of information on mixing effects, the application of multipliers to adapt single-species models, spatial-explicit models that account for individual intra- and interspecific competition (Cattaneo et al. 2017), or spatial-independent stand-level model separating the mode of competition (del Río et al. 2014) and process-based or hybrid models modified or created for specific mixtures to predict spatial and temporal dynamics (Forrester and Tang 2015; Forrester et al. 2017b).

One important challenge for multiple-species stands dynamics modeling is the application of 3D representation of trees that might better capture allometry changes and mixing effects on crown features (Barbeito et al. 2017). Other features that remain open is the correct modeling of recruitment and mortality (Porte and Bartelink 2002).

12.2.4.2 Bridging the Gap Between Research and Mixed-Forest Practitioners

Although the advancement of knowledge regarding mixed-species forest has augmented in the last decade, there are still many knowledge gaps and managerial questions that must be addressed. Coll et al. (2018) summarized this at the European level and pinpointed three important research gaps. Under the general recognition that mixed forests are more resilient than monocultures, there is an important lack of knowledge about which is the species composition that best provide resistance and recovery to disturbances. From a management perspective, more research is needed to confirm that mixtures allow for more options for adaptation to changing conditions and to elucidate which silvicultural systems are more appropriate to maintain the more resilient mixture.

Bauhus et al. (2017) and Pretzsch and Zenner (2017) suggested how to progress from the present accumulation of phenomenological findings to a design of mixed-species stands and advanced silvicultural prescriptions. They reviewed the mixing effects which are most relevant for suitable modeling, silvicultural designs, and the regulation of mixed stands as opposed to monocultures. They stress the key role of growth models, stand simulators, and scenario assessments for designing mixed-species stands. Silvicultural prescriptions derived from the scenario need to be both quantified and simplified for transfer to forest management and demonstrated in training plots.

12.2.4.3 Economic Valuation of Mixed Forests

Promotion of tree mixtures by owners and policy makers requires the identification of the economic benefits from mixed forests. Multiple-species forest yield a larger portfolio of ecosystem services that may reduce economic losses (Valsta and Jacobsen 2018) due to risk attenuation because of high diversification of potential financial assets (Knoke et al. 2008). However, the majority of economic studies on mixed forests have dealt with a single outcome, namely, timber, whereas attempts to include multiple outcomes are still scarce. One of the reasons for the difficulty to valorize mixed forests is the high level of externalities associated with mixtures. Landscape values, enhanced biogeochemical cycles, or climate regulation are difficult to monetize, although the common stakeholders' perception is that mixed forests can effectively deliver nonproductive services (Grilli et al. 2016). Nonetheless, one way to internalize externalities of these values is through the payment for ecosystem services scheme (PES) that has been considered to optimize the species mixture for climate regulation (Matthies and Valsta 2016).

12.3 Concluding Remarks

Research on mixed forests is gaining attention as mixtures are considered a valuable option to increase resilience and its constituent factors: resistance and recovery (Hodgson et al. 2015). The analysis of mixed-stands performance can provide reliable information about primary productivity to get a sustainable bio-economy strategy while preserving the species richness of forest ecosystems. EuMIXFOR has contributed to advancement of knowledge about mixed forests with important contributions to the analysis of productivity, stability, resource use, and characterization of mixed stands. EuMIXFOR has been a trigger point in the development of international research cooperation in science and technology following the mission of COST Association by building capacity, providing opportunities for early stage researchers, and increasing research impact.

During the last conference of EuMIXFOR held in Prague in October 2016 (http://www.vulhm.cz/en/eumixfor_final_conference), the following topics for the future of mixed forest research were identified:

- There is an urgent need for new experimental designs and long-term experimental sites across environmental gradients. The triplet-gradient analysis is a landmark example that should be extended to other species combinations and functional gradients worldwide.

- Effective modeling of mixed-stands dynamics requires combination of stand-level and individual neighborhood analyses (agent-based modeling) for understanding as well as enhancement of process-based models at the stand level for forecasting. However, models for mixtures should redefined assumptions, specifically light interception assumptions. The analysis of mixing effects should not be restricted to a single spatial or temporal scale.
- More research emphasis is needed on the relative importance of species identity effects on all ecosystem services to complement the analyses of diversity effects on forest functioning. More specifically, more knowledge is needed on the role species identity plays in the emergence of true mixing effects and that of differential functional traits to promote overyielding and stress tolerance in mixed versus pure stands.
- True mixing effects occur after removing confounding factors including past stand management and abiotic conditions. Any study aimed to uncover mixing effects should differentiate between structural diversity and species effect.
- Species proportion is dynamical, and it is better characterized by comparison with potential density corrected by area.
- There is a need for including uncertainties and considering a range of ecosystem services in the economic analyses of mixed forests. Reliable empirical statistical or process-based ecological models, designed for mixed forests, are needed to feed economic models.
- There appears to be a gap between policies supporting mixed forests and the ability of foresters to design and regulate mixed forests in practice. Implementation of knowledge transfer is needed.

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