



Conifer Defences against Pathogens and Pests — Mechanisms, Breeding, and Management

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Abstract

Purpose of Review Forestry in northern temperate and boreal regions relies heavily on conifers. Rapid climate change and associated increases in adverse growing conditions predispose conifers to pathogens and pests. The much longer generation time and presumably, therefore, lower adaptive capacity of conifers relative to their native or non-native biotic stressors may have devastating consequences. We provide an updated overview of conifer defences underlying pathogen and pest resistance and discuss how defence traits can be used in tree breeding and forest management to improve resistance.

Recent Findings Breeding of more resilient and stress-resistant trees will benefit from new genomic tools, such as genotyping arrays with increased genomic coverage, which will aid in genomic and relationship-based selection strategies. However, to successfully increase the resilience of conifer forests, improved genetic materials from breeding programs must be combined with more flexible and site-specific adaptive forest management.

Summary Successful breeding programs to improve conifer resistance to pathogens and pests provide hope as well as valuable lessons: with a coordinated and sustained effort, increased resistance can be achieved. However, mechanisms underlying resistance against one stressor, even if involving many genes, may not provide any protection against other sympatric stressors. To maintain the adaptive capacity of conifer forests, it is important to keep high genetic diversity in the tree breeding programs. Choosing forest management options that include diversification of tree-species and forest structure and are coupled with the use of genetically improved plants and assisted migration is a proactive measure to increase forest resistance and resilience to foreseen and unanticipated biotic stressors in a changing climate.

Keywords Conifer · Stress defence · Resistance breeding · Flexible management

Introduction

Conifers are some of the most successful lifeforms to evolve, having survived more than 300 million years of global change. The global distribution of conifers shows that they can thrive in many different ecosystems and under various stress conditions [1]. Clearly, their great ability to acclimate and adapt has contributed to their success.

As a result of past selection pressures, conifers have evolved diverse and effective defence mechanisms against insect herbivores, pathogens, and other heterotrophic

organisms. In recent decades, much of the biotic and abiotic damage in conifer forests can be related to ongoing global change. Global warming is increasing tree mortality both directly, through drought and heat stress, and indirectly by increasing the susceptibility to pests and pathogens [2]. In addition, global trade of plants and plant materials introduces pathogens and pests outside their natural range, where they may have devastating impacts on evolutionary naïve tree species [3]. This may have particularly severe consequences for trees, owing to their long generation times.

Forestry has long favoured conifers over native broad-leaf trees because of the high industrial value of conifer wood, coupled with the high productivity of conifer forests. Many conifer breeding programs were established after WWII to safeguard a stable supply of genetic material with improved properties for adaptation, productivity, and timber quality [4]. Most of the scientific research on conifers has focused on the north temperate and boreal zones, where

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conifer-dominated forests cover huge areas and form the basis of the forest bioeconomy. Here, conifers have been increasingly planted to the limits of their natural range and even beyond, into more temperate, northern, and alpine regions [5].

The aim of this article is to outline how conifer defences can be harnessed to enhance conifer resistance and resilience to native and introduced pests and pathogens (Fig. 1). We provide a short introduction of (1) conifer defence mechanisms and (2) conifer breeding for increased resistance towards biotic stressors, highlighting some of the success stories and challenges. Then, we (3) describe management practices to enhance the resilience of conifer forests to native and novel biotic stressors, and (4) outline some policy options and research needs to respond to both forecasted and unpredicted changes in biotic stressors.

Defence Mechanisms across Conifer Tissues

Conifer defence strategies involve a complex mixture of constitutive (performed) and inducible (acquired) defences [6, 7]. These defences, and their relative importance, can vary according to the species, tissue, genotype, environment, season, and tree age [6]. Constitutive defences are always present, even in the absence of an attack. Inducible defences are mobilized in response to attack or other external stimuli and can be directly induced, prolongedly upregulated, or latently sensitized (primed) [8, 9]. This wide range of defences, executed over different temporal and spatial scales, helps to protect conifers against diverse abiotic and biotic stressors.

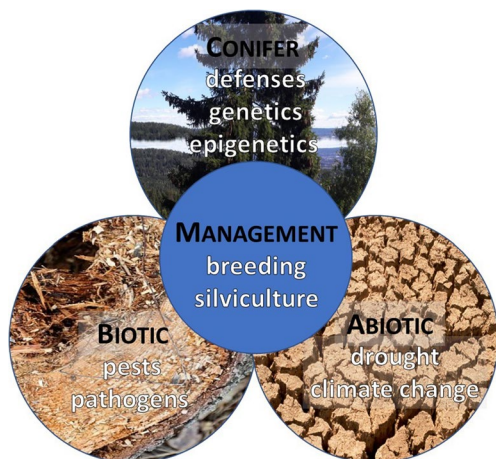


Fig. 1 In this review, we provide an overview of conifer defences, their genetic basis, and their interactions with biotic and abiotic stressors. This knowledge forms the basis for resistance breeding and silviculture-based integrated pest management practices to secure the future of sustainable forestry

Leaf Defences

Most conifers have needle-like leaves that are retained for several years as an adaptation to conserve resources. Needle anatomy, with some species-specific variation, reflects adaptations to harsh environmental conditions. Conifer needles are covered by a waxy cuticle that protects needles from environmental stressors like wind and drought. Cuticle waxes and other needle surface exudates also act as antimicrobials or make the leaf surface less wettable and thus suboptimal for spore germination [10].

Needle stomata control gas exchange and are used as entry sites by many pathogens [11] (Fig. 2i). The ability to regulate stomata closure is important to control water loss, and hence for drought tolerance [12] (Fig. 2a). Constitutively produced terpenoids and phenolics, as well as physical barriers such as lignified tissues, act as antifeedant defences against herbivores (Fig. 2e) or post-infection defences against microbes. For example, white spruce (*Picea glauca*) needles produce antifeedant phenylpropanoids, whose accumulation depends on tree phenology and genotype [13]. Induced defence responses in needles include production of phytoalexins, antimicrobial peptides, pathogenesis-related proteins, and generation of the hypersensitive response (HR), a rapid localized cell death at the site of infection (e.g. [6, 14, 15]). HR is generally associated with race-specific resistance to biotrophic pathogens, such as rust fungi (Fig. 2g), which derive their nutrition from living tissue [16]. A more comprehensive review of needle defence mechanisms has been provided by Fraser and co-workers [10].

Bark Defences

The bark is the first barrier against pests and pathogens attacking the main stem, roots, and branches of conifers. Cells and tissues involved in bark defences are mostly laid out in concentric layers around the circumference of woody organs [7]. Thus, attackers must overcome multiple defence barriers to reach the resources of the inner bark, cambium, and sapwood. The outer bark of conifers, the periderm, is composed mostly of dead cells rich in lignin and suberin, phenolics, and calcium oxalate crystals (Fig. 2k), forming a multifunctional barrier to various stressors [7]. However, loose cell aggregates called lenticels that allow for gas exchange may serve as entry points for small insects and pathogens [17].

In the inner bark (phloem), all conifers have constitutive physical and chemical defences that include lignified sclerenchyma cells, calcium oxalate crystals, and phenolic bodies [18]. Axially oriented phloem parenchyma cells,

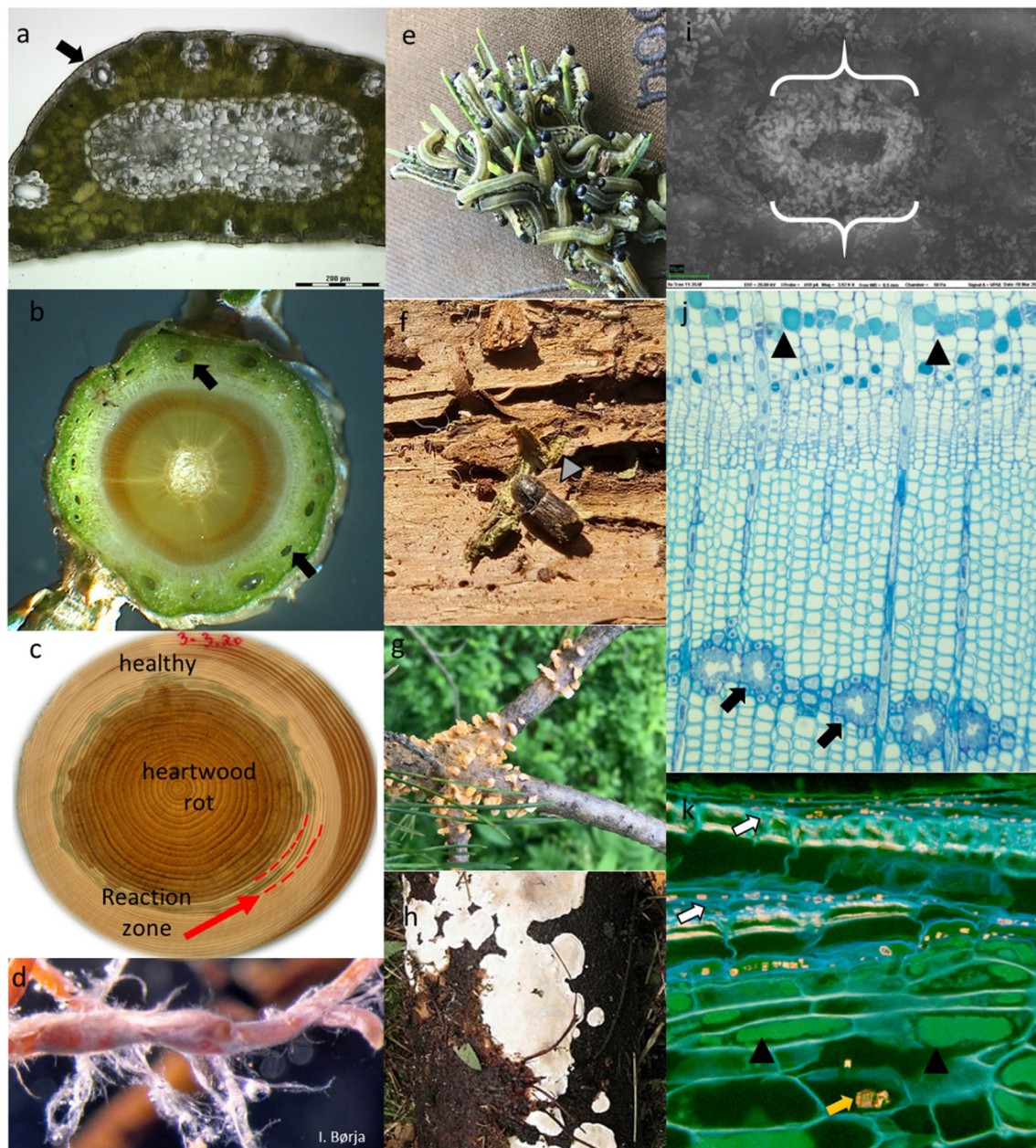


Fig. 2 Examples of conifer tissues and defence mechanisms. Conifers must protect their needles (**a**), stems (**b**, **c**), and roots (**d**) from many different pests and pathogens. These attackers include defoliators such as sawflies (*Neodiprion sertifer*) (**e**), bark beetles (*Ips typographus*) (**f**; grey arrowhead), rust fungi (*Cronartium pini*) (**g**), and root rot fungi (*Heterobasidion parviporum*) (**c**, **h**). Conifer defences include a waxy cuticle preventing pathogens from entering needles through stomata (**i**; white brackets); specialized cells that produce and store toxic phenolics (**j**, **k**; black arrowheads indicate polyphenolic

cells) and terpenoid resin (**a**, **b**, **j**; black arrows indicate resin ducts in needles, young stems, and sapwood, respectively); compartmentalization of pathogens through formation of a chemical barrier or reaction zone (**c**; red arrow); cell wall lignification and suberization to physically protect cells from penetration (**k**; white arrowheads), and calcium oxalate crystals (**k**; yellow arrow) interfering with feeding by chewing pests. Interactions with beneficial microbes, such as ectomycorrhiza (**d**), may also improve the resistance and stress tolerance of conifers

called polyphenolic parenchyma (PP) cells, are specialized for synthesis and accumulation of phenolics (Fig. 2j) [19, 20]. PP cells and radially oriented ray parenchyma, which also serve as storage sites for starch, are involved in radial and circumferential transmission of signals that

activate inducible defence responses [6]. Numerous symplastic cell junctions (plasmodesmata) facilitate transport of signal molecules and nutrients between and among PP cells and ray cells [7].

All conifers in the pine family also have radial and/or axial resin ducts, resin blisters, or resin cells [7] with epithelial cells that accumulate terpenoid resin internally or secrete it into the duct/blister lumen (Fig. 2b). Terpenoid resin is a diverse mixture of monoterpenes, sesquiterpenes, and diterpenes and serves as a chemical and physical defence against pests and pathogens [21]. When the bark is wounded by an insect, fungus, or physical damage, the pressurized resin can repel, trap, or kill the organism and seal the wound. More detailed reviews of defence mechanisms in conifer bark have been published [4, 16, 19].

The roles of terpenoids in conifer resistance to bark beetles are particularly well studied. Zhao and co-workers [22] demonstrated a dose-dependent relationship between inducibility of terpenes and tree resistance to bark beetle mass attack. Other studies have shown a positive relationship between resin duct size and tree survival during a bark beetle outbreak [23]. However, all tree-killing bark beetles, such as the European spruce bark beetle (*Ips typographus*) (Fig. 2f), vector ophiostomatoid fungal symbionts that can detoxify terpenes into compounds acting as bark beetle attractants and may thus contribute to beetle attack success [24]. Additionally, drought and elevated temperatures may affect the composition and amounts of volatile terpene emissions and thus facilitate bark beetle mass attacks [25••]. Details on the complex environment-conifer-bark beetle-fungi interactions have been reviewed in earlier publications [24, 25••].

Xylem Defences

More than 90% of conifer xylem is composed of tracheids, hollow conduit cells interconnected through pits, enabling slow but robust water transport [26]. Trees with small tracheid pit apertures, high pit aperture resistance, and large valve effect are more resistant to drought- and freezing-induced embolism, i.e. blocking of water flow by an air bubble or cavity [27]. Tracheids have a thick secondary cell wall, where structural carbohydrates (cellulose and hemicellulose) are covalently linked with lignin, a complex phenolic polymer. Because tracheids undergo genetically programmed cell death soon after maturation, they have no induced defences. However, due to its molecular architecture, lignin is highly recalcitrant to degradation [28]. Microbial access to the structural carbohydrates in the tracheid cell walls requires degradation or modification of lignin, something white rot and brown rot fungi, respectively, are capable of (Fig. 2c and h).

Depending on the conifer species, up to 10% of the xylem is composed of thin-walled parenchyma primarily associated with radial rays running from the phloem and deep into the xylem. Parenchyma radial rays play a major role for storage and transport of water, nutrients,

and non-structural carbohydrates, thus regulating xylem hydraulics, growth, and active defences. Many pathogenic fungi gain access to the xylem via bark wounds, which trigger the formation of traumatic resin ducts within the new annual ring in many conifers [20]. Traumatic resin duct formation can also be induced by pest attack or application of the defence hormone methyl jasmonate [29•]. In conifers with constitutive or induced xylem resin ducts, ray parenchyma and axially orientated resin ducts may form an interconnected network for defence signalling, biosynthesis, and translocation of defence metabolites [20, 30]. The extent of this network and the nature of the induced defence metabolites differ considerably between tree species [31•], probably because of adaptation to different selection pressures. Parenchyma cells in the water-conductive sapwood live for several decades, until the innermost sapwood is transformed to dead heartwood. During heartwood formation, the ray's energy reserves are metabolized into protective heartwood extractives, such as polyphenolics and terpenes [32, 33]. The durability of heartwood towards wood decay is largely determined by the amount and antimicrobial and antioxidant properties of these extractives [34].

Wood decaying basidiomycetes, like *Heterobasidion*, have an optimal moisture content ranging between 40 and 80% [35]. In addition to the correct moisture, wood decaying fungi need oxygen for expression and activity of lignin and phenol degrading enzymes important in their colonization [36]. In Norway spruce, the moisture content of sapwood and heartwood is 150% and 50%, respectively, while seasonal fluctuations in oxygen healthy sapwood [37] and heartwood [38] are similar. It is challenging to determine the extent to which oxygen content varies between specific cell types (living parenchyma vs. tracheids) or within the wood microspatial, but high water content in the lumens of sapwood tracheids could be envisaged to displace oxygen at microsites in the secondary cell wall where decay processes occur. In line with this reasoning, many pathogenic wood decay fungi prefer to colonize heartwood in conifer species with non-resinous heartwood, such as species of *Picea* and *Abies*. When a heartwood-based fungal colony attempts to expand laterally, the tree forms an extractive-rich xylem defence zone at the interface between the dead heartwood and the live inner sapwood. This reaction zone is characterized by tracheids and ray cells that become filled up with phenolic compounds and terpenoids (Fig. 2c) [33, 39] and may also include dense rows of traumatic resin ducts [33]. The reaction zone forms a barrier against radial fungal spread into the sapwood, as described in the CODIT (compartmentalization of decay in trees) model [40]. More detailed descriptions of xylem defence mechanisms have been provided by, e.g. Morris and co-workers [29•] and Pearce [33].

Genetic and Epigenetic Regulation of Conifer Defences

The draft Norway spruce genome, released in 2013, was the first conifer genome to be published [41]. Conifer genomes are extremely challenging to study because of their huge size (20–30 gigabases) and long stretches of highly repetitive DNA [42]. However, rapidly improving sequencing and bioinformatics tools are now helping us unravel these giant genomes [43–45••].

Many defence-related genes have been identified in conifers, especially genes involved in biosynthesis of terpenes and phenylpropanoids [46, 47]. Concerning terpene production, the ability to rapidly increase gene expression can be related to resistance [48]. High heritability estimates for resistance and much intraspecific variation in resistance phenotypes indicate that terpenes and other defence compounds are under strong genetic control [49]. Like most adaptive traits, conifer defence traits have a polygenetic basis and are determined by the action of many different genes [50]. The polygenetic nature of conifer defences partly explains why defence traits generally confer partial, and not complete, resistance to pests and pathogens [51••]. Additionally, conifer defence genes are over-represented among highly polymorphic genes, indicating that they can be useful for population genomic studies of stress adaptation [52]. Recently, 30–50-kb single nucleotide polymorphism (SNP) arrays for conifer genotyping have been developed [43, 53–56]. These arrays will aid conifer breeding programs by facilitating genomic predictions and selection of new parents to create more resistant offspring.

Epigenetics is the study of changes in gene expression that are due to DNA methylation and histone methylation or acetylation but involve no alterations of the DNA sequence. Epigenetic modification regulates gene expression by determining which DNA regions are open to be transcribed. Changes in epigenetic modifications can be triggered by abiotic factors, like temperature and light, or biotic factors, like pathogens, pests, and beneficial microbes [57]. These modifications can result in stable phenotypic changes within an individual and be passed on to subsequent generations [58, 59]. Thus, epigenetic mechanisms may allow rapid adaptation to the environment [60].

We are just beginning to understand the role of epigenetics in conifer adaptation. The best evidence for the importance of epigenetics in environmental adaptation is from 40-year-long studies in Norway spruce [59]. Clonal progenies produced from zygotic embryos at 18 or 30 °C show long-term differences in the timing of bud set and flushing, indicative of an epigenetic memory [61]. Under natural conditions, progenies from warm seed years become better adapted to prolonged growing seasons [62], likely without any major change in allele frequencies. Recent research also points to the involvement of DNA methylation in long-term induced resistance

and defence priming of Norway spruce [8, 9]. However, more research is needed to understand what epigenetic mechanisms and machinery are important in conifers and if phenotypic plasticity resulting from epigenetic regulation shows genetic variation that can be selected for [63].

Breeding for Pest and Pathogen Resistance

Managing diseases and pests of conifers by breeding trees for increased resistance is of great interest [64]. Resistance can be defined as the ability of a tree to limit or suppress the growth and development of a pathogen or pest, or to prevent attacks altogether. Resistance is thus an observable phenotype that results from the interaction between the tree and a pest or pathogen in a given environment [51••]. Ultimately, a certain level of resistance is a prerequisite to survive long enough to reproduce and pass on genes to the next generation. The mechanisms involved in interactions between trees and pathogens/pests reflect past selection pressures, such as whether the tree population and the biotic stressor share a co-evolutionary history. The outcome of these interactions is also influenced by abiotic conditions: environmental conditions can modify the phenotypic resistance, e.g. by causing changes in the pest or pathogen population or by influencing tree defences. Tree resistance may also depend on ontogeny. For example, older trees may be able to fight off a specific attacker through a certain combination of constitutive and induced defences, whereas young seedlings may lack crucial defences and succumb. Finally, increased allocation of resources to resistance may come with a cost to growth and reproduction [65]. The strength of this allocation trade-off depends on species and environmental conditions [66]. All this complexity has important consequences for breeding programs aiming to balancing selection of resistance traits with the other important traits and maintaining genetic diversity.

Conifer Breeding

A traditional conifer breeding program usually starts with a phenotypic “plus-tree selection” of the largest and best-looking trees from a base population of naturally regenerated or planted trees (process summarized in [4]). The plus-trees are grafted into breeding arboretums or seed orchards for mating and seed production. Their progenies are evaluated under field conditions to obtain breeding values for selection of the best parents for the next breeding cycle and more advanced seed orchards. The first breeding cycle, which normally screens for variation among half-sib families with large genetic diversity (e.g. from open pollination), usually takes 10–15 years. This is estimated to be the optimal age for selection for height growth, a proxy for volume production when “genetic gain per unit-of-time” is considered

[67]. Variation in resistance and response to many biotic and abiotic stressors can usually also be observed within this time. Some breeding programs choose to delay the first selection until the age of 20–30 years to be able to differentiate and evaluate traits that are expressed later, such as longer-term productivity, adaptation, health, and wood quality. Many conifer breeding programs around the world have finalized the first selection cycle [68].

Picea species are easy to propagate vegetatively. Therefore, for the second breeding cycle of a given breeding population, clonally replicated long-term field experiments have been established for the most promising 30–40 family members selected from nursery tests [69]. When the same genotypes are planted across a range of environments, such trials provide information about the phenotypic plasticity and stability of individual genotypes [4]. The drawbacks of traditional breeding strategies are that field testing is laborious and limited to a few (often four) sites, and careful selection of these sites might be critical to capture sufficient exposure to relevant stressors [4]. As climate change is already predisposing trees to various biotic stressors, important flexibility can be added to breeding programs by maintaining the initial progeny trials as genetic resources even if the breeding cycle seems completed [70]. Novel stressors might reveal new phenotypic variation and new phenotyping and genotyping methods may add new and valuable data.

Genetic diversity is a necessary resource for the long-term evolution of species, and an “insurance” of a forest’s

survival and productivity, especially regarding climate uncertainties [71•]. Diversity must also be kept through the cycles of resistance breeding. It is therefore important that the breeding strategies allow selection at a sufficiently high intensity while maintaining the effective population size. There might, however, be trade-offs between the goal of improvement and diversity [64].

For resistance breeding, one can consider two different main strategies for selection (Fig. 3). In many large breeding programs, in situ selections are made of the largest, most vital, and healthiest trees, under the assumption that this will increase the total performance as an effect of the accumulation of beneficial gene variants over generations [72••]. Alternatively, selection could be trait-based, e.g. when the critical traits are known for the targeted resistance [72••]. These strategies are not mutually exclusive, but serve as a basis to orient subsequent discussion. In some situations, strategy 1 could be the initial step of a breeding program, while strategy 2 is used when the selection for the breeding population is made and more knowledge about the traits and their genetic control has been established.

Breeding for Increased Resistance in Conifers — Lessons, Challenges, and Opportunities

Screening of genetic variation for increased resistance has been conducted for many pest- and pathosystems in

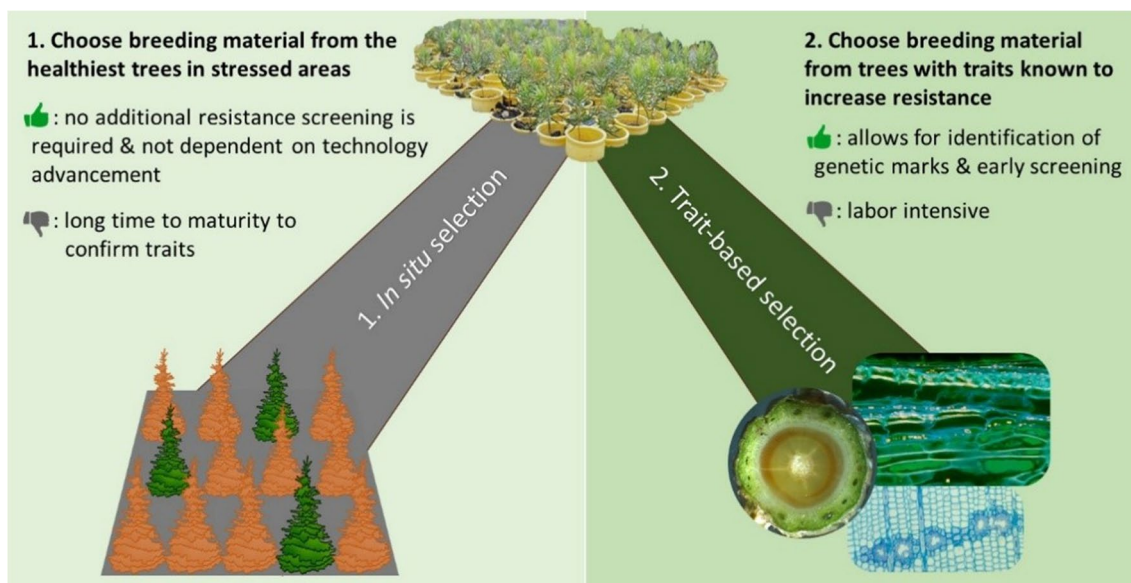


Fig. 3 Two “roads” to increased resistance through breeding: (1) in situ selection of trees with proven or suspected resistance in the field and (2) selection of trees possessing traits that are known to confer resistance. The premise for using strategy 1 is high and even pressure by the stress factor over the site. Otherwise, it is difficult to distinguish between candidate resistant trees and trees with stochastic

escape of the stressor. For stressors with uneven spatial patterns in a forest, and moderate or weak effect on the tree vigour and survival, such as many root- and heartwood decay pathogens that spread via root contacts between neighbouring trees and native and novel pathogens and pests in a build-up phase of attack pressure and epidemic, strategy 1 is poorly applicable

conifers [73], but with variable success so far. Here we present some examples of these efforts and describe the lessons learned and challenges faced. In summary, the most successful breeding efforts deal with pathosystems where genetic variation in resistance can be selected in seedlings, allowing for effective screening of many individuals. The later in development genetic variation in resistance can be screened, the more will environmental factors influence the response, and time delays in testing and phenotyping will slow down the breeding cycle. However, when to perform screening depends on the existence of knowledge about traits that correlate with resistance in the particular pathosystem or tree-pest interaction and the developmental stage of the tree species.

All North American white pines are highly susceptible to blister rust caused by *Cronartium ribicola* believed to originate from eastern Asia. This biotrophic fungus was accidentally introduced to North America around 1900 and is causing massive mortality that can exceed 95% in some populations [71•]. This has prompted extensive research to identify trees with natural genetic resistance to blister rust. Tree resistance to white pine blister rust can be reliably determined in young seedlings, enabling high-throughput screening methods that use spore inoculation of seedlings to mimic natural infection. The breeding process is further facilitated by the possibility to select candidate parental trees from stands suffering epidemic infection levels of this windborne and outcrossing pathogen. Major gene resistance (MGR) has been documented in four white pine species, and some level of quantitative resistance (QR) is likely present in all species [71•]. As a result of the effective breeding progress, resistant offspring are used extensively for reforestation and restoration of white pine stands [71•]. However, in sugar pine (*Pinus lambertiana*) and western white pine (*Pinus monticola*), MGR is sometimes overcome by virulent blister rust strains. Therefore, incorporation of multiple MGR- and QR-based partial resistances in elite seed orchards are needed to obtain long-term, durable resistance [73].

Another pathosystem for which increased resistance has been achieved via breeding is infection of Port-Orford cedar (*Chamaecyparis lawsoniana*) by the introduced water- and soilborne oomycete *Phytophthora lateralis*, first discovered in a North American nursery in 1923. The first testing of *C. lawsoniana* for genetic variation in disease resistance was carried out in the 1980s. Relatively resistant parents were crossed, and progeny resistance was screened by dipping the root system of young seedlings in a pathogen spore solution and monitoring mortality for up to 3 years. This screening revealed both MGR and QR towards *P. lateralis* in Port-Orford cedar. Impressively, resistant seed lots were available for seven out of 10 breeding zones within 10 years of program initiation [74]. This success story is very encouraging for those engaged in disease resistance breeding of conifers [72••].

Norway spruce (*Picea abies*), the dominant conifer in Northern Europe and subalpine areas of the Alps and Carpathian Mountains, is heavily affected by pathogenic white rot fungi in the genus *Heterobasidion*. All three *Heterobasidion* species indigenous to Europe can establish in roots and stem heartwood of this low-resinous conifer. Since the late 1990s, several studies have demonstrated heritable genetic variation in resistance against *H. parviporum* [75–77]. In these studies, resistance phenotyping was based on lesion lengths in the phloem and the extent of axial fungal growth in the sapwood in stems or branches of artificially inoculated seedlings and saplings. One lesson from these experiments is that the ontogenetic stage of the tree at the time of inoculation influences tree-pathogen and genotype × environment interactions [75, 77]. Some genes associated with QR in this pathosystem are involved in lignification and synthesis of catechin and lignan [76, 78]. The QR in Norway spruce towards *Heterobasidion* species does not confer any broad-spectrum resistance towards other necrotrophic pathogens, as Steffenrem and co-workers [79] found no correlation in phloem lesion lengths between *H. parviporum* and *Endoconidiophora polonica*, a pathogenic blue-stain fungus vectored by *Ips typographus*. Similarly, Capador-Barreto and co-workers [78] found that the genetic basis of QR in Norway spruce differs between *H. parviporum* and *H. annosum* even though these pathogens occur together in many regions. Selection of QR markers that are shared between such sympatric pathogens might be the best strategy for successful resistance breeding against *Heterobasidion* species [78].

While we are not aware of any conifer breeding programs for resistance against bark beetles, there are large differences among genotypes in resin duct production, a trait known to correlate with bark beetle resistance [66]. There is, thus, evidence suggesting that resin duct characteristics are heritable and subject to genetic control [66]. This may pave the way for resistance breeding aimed at resin-based defences. However, breeding for increased resin production might have undesirable consequences for the wood-processing industry. At a more fundamental level, breeding for tree resistance against bark beetle attack might be difficult due to the stochastic nature of how the beetles select trees for mass attack. First, beetles tend to attack trees suffering from acute stress, which may result from biotic or abiotic disturbances rather than any heritable tree defence traits. Second, the beetles' pheromone-mediated mass attack behaviour means that trees may be attacked and overwhelmed by the beetles simply because they grow next to a susceptible tree. Finally, the stochastic occurrence of abiotic disturbances may provide ample proliferation material for the beetles, even in stands with genetically resistant trees.

An alternative strategy to increase conifer resistance or resilience to bark beetles would be to breed for increased tree resistance to abiotic stressors, such as drought, that

predispose trees to bark beetle outbreaks. This would require vitality phenotyping of mature trees growing in areas prone to drought. So far, genotyping arrays including tens of thousands of SNPs have failed to find genes of major importance to drought tolerance in conifers. This may be because the sparse genomic coverage and the low linkage disequilibrium of such arrays make it difficult to capture the relevant variation in genomic data [80]. However, there is some evidence of genetic and heritable variation in drought tolerance in many conifer species, indicating that there is a potential for selective breeding [57, 74].

Breeding strategies that are under development and evaluation include the use of genomic data to predict genomic breeding values [80–83], to reconstruct a pedigree, or to calculate a genomic relationship matrix for quantitative prediction of breeding values [84, 85]. High-quality phenotypic data are necessary in all cases. However, for the genomic prediction, phenotypic data are only necessary under the development of the prediction model. For relationship-based methods, such as genomic best linear unbiased prediction (GBLUP) [84], phenotypic data is always required. These emerging strategies show particular promise in enhancing existing breeding systems by reducing the requirement for expensive controlled crosses and establishment and maintenance of trials.

Genomic prediction still needs to be sufficiently validated for conifer breeding. However, two relationship-based approaches that have already proven efficient in breeding are the “Breeding-without-breeding” [86] or “quasi-field trial” [87] strategies based on pedigree reconstruction. In short, these strategies utilize existing plantations established with material from seed orchards or breeding arboretums. Meaning, there is kinship information for these stands, but they were not necessarily established as designed trials. Spatial statistical methods are used to even-out the environmental variation observed among the phenotypes. Using phenotyping to identify the most vital and healthy trees in the population, genotyping to map the relationship structure of these select trees, and quantitative statistical methods, “ad hoc progeny trials” can be established wherever the material is planted [88]. These strategies do not require any established association between traits and genes, or genomic prediction models. They are flexible for the breeders to exploit large populations planted across environmentally variable landscapes and stress, in order to make in situ selection [89] (Fig. 3). The time from initiation of a program to selection for a new seed orchard can be as short as a few months. However, the approach requires that the stands are genetically diverse, and that information about deployed genetic materials at a site level is available.

Integrating Tree Resistance and Silvicultural Practices for Increased Resilience to Climate Change

Given the challenges posed by climate change, it is crucial that forest health perspectives are closely aligned with silvicultural practices [90]. Two approaches have been proposed to address risk management in forestry: anticipation and mitigation of risks (risk reduction) or promotion of forest resilience, i.e. the ability to absorb perturbations and maintain desired properties [91] (Fig. 4). The former involves management options that can be implemented already in forest nurseries, whereas in forest stands the applicability of each approach depends on the chosen regeneration/management regime.

Forest Nurseries

Integrating genotypes selected in breeding programs into silvicultural practices begins in the forest nurseries. Additionally, nursery production of large quantities of high-quality conifer seedlings is required to meet global forest demands [92]. Production of quality plants for reforestation entails that nurseries are aware of the genetic and physiological characteristics of each propagated species and genotype [92]. For example, nurseries must choose seed from seed sources

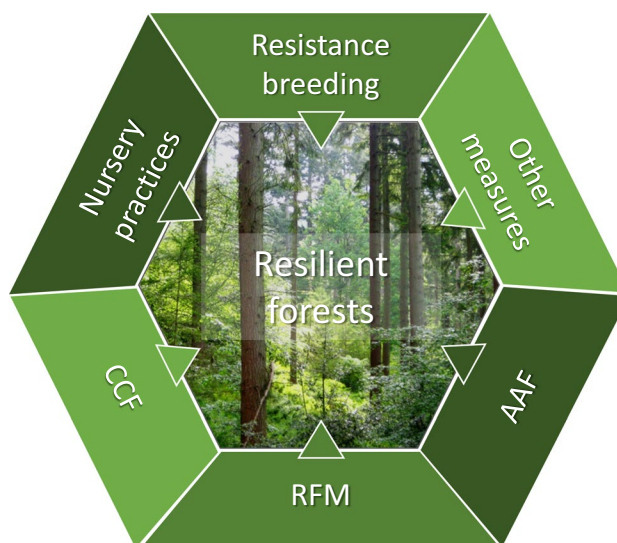


Fig. 4 Multiple forest management practices are required to foster flexible and adaptive forests that are resilient to increasing pest and pathogen pressure as well as climate change. These management practices include breeding for stress-resistant genotypes, regenerating with a suitable mix of tree species for the environment, choosing an appropriate forest management strategy for the stand, and implementing proactive forest policies. CCF, continuous cover forestry; AAF, any-aged forest management; RFM, rotation forest management

with a level of cold adaptability appropriate for the location they supply saplings [70]. Production of quality seedlings also requires ample water, fertilizer, and pesticide as seedlings can be particularly vulnerable to drought, nutrient, and pathogen stress [93]. One way to reduce nursery reliance on fertilizer and improve plant growth and resistance to disease is to use symbiotic, epiphytic, and endophytic microbes [93]. In recent years, it has been proposed that the microbiome also increases host disease resistance through direct antibiosis, physical protection of the roots, or effects on host defences [94, 95]. The specific associations between conifers and their microbial symbionts depend on tree species, genotype, organ, age, nutrient status, and environmental conditions [96, 97]. The best-studied conifer microsymbionts are ectomycorrhizal fungi (Fig. 2d), which aid nutrient acquisition and growth [98], especially under nutrient-poor conditions [96]. Long-term studies by Gehring and co-workers on pinyon pine (*Pinus edulis*) showed that tree selection of ectomycorrhizal partners is genetically based and heritable, and that drought-tolerant trees have different ectomycorrhizal fungi than drought-intolerant trees [99]. The obvious place to recruit beneficial microbes in forest management is forest nurseries, where desirable microbes can be introduced to increase out-planting success and growth performance of conifers on poor sites, as has been demonstrated with the mycorrhizal fungus *Pisolithus tinctorius* [100]. The primary obstacle in incorporating mycorrhiza in nursery production is that the heavy usage of pesticide and fertilizer in nurseries disfavours ectomycorrhization, but ectomycorrhization is needed to reduce the dependence on these chemical products [96]. Additionally, because seedlings usually are planted in a wide range of site and soil conditions, implementing mycorrhiza in seedling production would probably require site-specific tailoring of mycorrhizae [101].

Rotation Forest Management

The forest management practice involving establishment/regeneration, thinning, and clear-felling, referred to as rotation forest management (RFM) or even-aged management, originated in the eighteenth century in Germany during a period of rapid industrialization and impending timber shortage. The transition to RFM involved clearing of native hardwood and mixed hardwood/conifer forests and planting of fast-growing monocultures of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) [102]. RFM has been widely adopted in continental Europe [103]. In the Nordic countries, where most of the native forests are coniferous, RFM was adopted relatively late, but is today the standard silvicultural practice [104].

Irrespective of the management practice chosen, it is imperative that tree species requirements are matched with site conditions to reduce the risk that abiotic stressors will

predispose trees to pathogens and pests. In the last decades, it has become painfully evident that forest susceptibility to disturbances such as windthrows, bark beetle outbreaks, and wood decay increases with forest age. In a modelling-based study, Zimova and colleagues found that simply reducing the rotation length probably will not be sufficient to manage increasing frequency and intensity of disturbance events [105]. Instead, they suggest that a combination of management measures is needed to reduce risks and enhance forest resilience. At the landscape level, increased mixing of stands with different tree species and age classes is a promising approach to improve forest resistance and resilience and avoid large-scale disturbances by biotic stressors and predisposing abiotic factors [106]. At the stand level, a meta-analysis of over 600 studies showed that when a tree species is grown in mixed conditions it is less likely to be damaged by a given specialist insect herbivore than if it is grown in a pure stand [107]. This phenomenon is known as associational resistance [108]. Even though admixtures of tree species are generally positive, certain combinations of tree species, such as those of alternate hosts of rust fungi, can be disastrous. Additionally, the optimal spatial agreement of tree species is not always clear. As a disease example of the benefits of tree species admixtures, mature Norway spruce stands in Fennoscandia are often heavily infested by *Heterobasidion parviporum*, which spreads via root contacts between neighbouring spruce trees. To limit infection after regeneration, it is recommended to switch tree species or establish a mixed species forest in infested stands. However, due to the lack of commercially valuable alternative tree species that are suitable for Norway spruce sites, many forest owners continue to plant Norway spruce despite the predicted increase in decay frequency in the next tree generation.

RFM comes with several options for risk reduction, whereas options for promoting forest resilience are more limited in even-aged, monoculture forests. In anticipation of a warming climate, managers can adjust tree species composition and select for individual traits, such as longer growing season and drought tolerance, in high-risk sites by planting species, migrated provenances or seedlings from breeding programs [91]. Greater tolerance to abiotic predisposing factors will likely contribute to increased biotic stress resistance.

It is well documented that endo- and epiphytes can have antagonistic effects on other microorganisms. A large proportion of endophytic fungi (80%) produce biologically active compounds with antibacterial, fungicidal, and herbicidal activities. Endophytes can also increase tree resistance to pathogen infection [109]. Most foliage endophytes have a wide host tree range, although, endophyte community composition varies with host tree [110]. Beneficial effects of increased endophyte diversity provide another mechanistic

explanation for why mixed forests tend to have increased resilience to pest and pathogen attack.

Continuous Cover Forestry

Forest management practices falling under the umbrella concept of continuous cover forestry (CCF) or uneven-aged management gained momentum in the 1980s, following large-scale mortality in Central-European conifer forests, attributed to complex interactions between air pollution, soil acidification, and biotic stressors [102]. CCF usually involves the use of natural regeneration, selective harvesting, and clear-fellings with a gap size below 0.25 ha [111]. There are no solid data about the share of European forests that are managed through CCF, but Mason and co-workers [103] estimated that it could be as high as 30%. In the Nordic countries, CCF has long been treated with scepticism by forest managers [112, 113], but lately there seems to be an increased interest in the practice [114]. Although CCF is not a novel concept, there is little documented information about the resistance and resilience of CCF forests to disturbances, owing to the relatively recent adoption of CCF at a wider scale. However, CCF forests tend to be admixtures of conifers and broadleaved trees, and the benefits of tree species mixtures may also apply here. The structural diversity of CCF forests in terms of tree species and age likely increases their ability to absorb perturbations associated with storms or bark beetle outbreaks. However, uneven-aged CCF management strategies maintaining continuous Norway spruce regeneration will favour the spread of *H. parviporum* between trees of different size classes [115]. This negative effect is exacerbated by the difficulty to conduct forest operations without damaging the roots of the remaining trees, providing additional entry points for the root rot pathogen. If CCF is based only on natural regeneration, it has been questioned whether CCF could compromise the adaptive capacity of the forest ecosystem [116]. However, rapid epigenetic adaptation of forest trees might provide a solution to problems such as temperature and drought stress [59, 61, 117].

Any-Aged Forest Management

An approach referred to as any-aged forest (AAF) management [118] or freestyle silviculture [119] is a kind of hybrid between RFM and CCF, as it will consider all silvicultural options at any stand state. AAF management may include prolonged periods of uneven-aged CCF, but if natural regeneration fails regeneration methods of RFM can be used [118]. Another advantage of AAF is that it allows adaptation of forest management at micro-spatial scales within a stand. This could for instance be to change the tree species composition

through planting in pockets infested by pathogenic wood decay fungi with high host specificity. Additionally, the shade-response strategies of the tree species need to be considered as there is some evidence that defence-responses may be effected by shade tolerance [120]. For example, the North American white spruce (*Picea glauca*) thrives and is less defoliated by spruce budworm in the mixed-wood, semi-shaded conditions provided by CCF [121, 122]. Other species, like red pine (*Pinus resinosa*) and Douglas-fir (*Pseudotsuga menziesii*), require full sun and may be better adapted for RFM [123]. Thus, it is important to take into consideration the silvicultural properties of the desired conifer species when choosing the forest management strategy. Woods and co-workers concluded that proactive and flexible management options, like AAF, may be the best way to promote forest resilience to insects and diseases in the face of the uncertainties presented by climate change [90].

Conclusions and Perspectives

Rapid changes in climatic condition and associated stressors, including introductions of non-native pathogens and pests, are increasingly challenging RFM. As highlighted in several critical reviews, forest managers and policy makers must now prepare for events that lie outside the range of past experiences [90, 124].

There is obviously both regional and local variation in the nature and potential impact of different biotic and abiotic threats to forest health. Conifers that have been planted at sites they are poorly adapted to, or are growing at the latitudinal or altitudinal margins of their natural range, will be subjected to disturbances that can surpass past experiences. The magnitude of these disturbances also depends on how past management has shaped the forests at the landscape level. While milder winters contributed to enormous outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) in British Columbia, it was pre-existing landscape conditions, involving several-fold increase in volumes of susceptible host tree over the previous century, that enabled the unprecedented scale of the outbreak [90]. In Europe, Norway spruce has clearly been following a similar trajectory in many regions.

Based on the sound principle that “prevention is better than cure”, policies and forest management practices should aim to prevent disturbances rather than to address them once they occur [124]. Diversification of forests, in terms of tree-species composition and forest structure at the landscape level, has been proposed as a proactive measure to increase forest resistance and resilience (Fig. 4). Lately, there has been a trend towards deregulation of forest policies in Europe and different countries still show a wide variation in recommended management options [125]. In order to mitigate damage caused by bark beetles, expert

groups have recommended to adopt legislation that allows the implementation of a broader spectrum of forest protection measures [5]. Europe is seeing an increased interest in alternative forest management practices, but so far there are few lessons available on how these practices affect forest health. To enable active learning and adaptive forest management, we need more research on factors that affect forest resilience and resistance under different management regimes, including forest health monitoring and pathogen/pest modelling [126••].

Maintaining sufficient genetic diversity in conifer forests is a prerequisite to sustain their adaptive capacity. Preservation of genetic diversity is a risk-spreading strategy also for planted forests. Hence, it is important that conifer seed orchards produce outcrossed progenies from a sufficient number of parents with little or no relatedness [4], and that vegetatively propagated materials include a sufficient number of genotypes. Maintaining additive genetic variation is also crucial for long-term, multi-generational breeding efforts to produce genetic gains in adaptive traits and performance traits [4]. Therefore, breeding strategies usually define the size of a breeding population, after the initial selections from the first breeding cycle, to around 1000 individuals [4]. Finally, since many managed conifer stands still deliver ecosystem services close to the natural situation, forest plantations with improved genetic material must also fulfil these ecological functions (Fig. 4).

There are still only a handful of examples of successful breeding of increased resistance to biotic stressors in conifers. This may be due to several reasons, such as a lack of coordinated efforts with long-term commitment and low heritability and frequency of resistance traits in the trees [68]. Ineffective methods to detect genetic variation in resistance to a specific stressor may be an additional reason; Pike and co-workers describe how breeding for increased resistance in eastern white pine (*Pinus strobus*) to *Cronartium ribicola* initially was hampered by poor screening methods that failed to generate meaningful data because either too many or too few seedlings were killed [72••]. Refinement of the phenotyping protocol revealed significant heritability for resistance and changed the trajectory of the breeding program [127]. More collaboration in resistance breeding between countries facing similar challenges is needed, as this will allow for allocation of sufficient resources and a sustained effort over time. However, resistance breeding alone is not a silver bullet that will provide rapid solutions to future challenges. Breeding should rather be seen as part of an adaptive forest management strategy involving many approaches (Fig. 4). Breeding remains a slow process and it takes at least 10–20 years before operational planting of resistant material can start. However, with an increased understanding of the genetic basis of tree resistance and the feasibility of genome-based selection methods, there is hope that resistance breeding can be accelerated in the near future.

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