Constraints and Trade–Offs in Mediterranean Plant Communities: The Case of Holm Oak–Aleppo Pine Forests

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I. Abstract

In this paper we review those aspects that are relevant to the development of a mechanistic ecological theory to account for the structure and dynamics of Mediterranean forests, focusing our attention on mixed forests of holm oak (*Quercus ilex* L.), a shade-tolerant, slow-growing species that resprouts vigorously after disturbance, and Aleppo pine (*Pinus halepensis* M.), a fast-growing, nonresprouting, shade-intolerant species. The main objectives of this report are: to introduce some of the primary features of these forests, showing their structural complexity and historical peculiarities; to show that much of this complexity can be conceptually reduced to two main factors of variation, soil-moisture gradients and a complex interaction of historical management and disturbance regimes; and to contrast the unique features of Mediterranean systems with other communities that have inspired generalization in ecology.

Plants in Mediterranean-climate regions must face several environmental constraints during their life cycle: water limitation, competition for light, and a complex set of disturbance regimes, mainly fire, herbivory, and human exploitation. The response of co-occurring species to a given set of environmental constraints depends on a combination of physiological and morphological traits. In holm oak–Aleppo pine forests, the lower limit of distribution along a soil-moisture gradient appears to be controlled by dry-season water stress on seedling performance, and the upper limit seems to be controlled by shade tolerance relative to competitors. The processes that generate and maintain these patterns are related to the responses of the two species to the water and light environments that result from interacting gradients of disturbance and resource availability.

The dynamics of mixed holm oak–Aleppo pine forests may be represented along two major environmental axes: water availability and light intensity; namely, time since last disturbance. At the regional scale, the presence of holm oak and Aleppo pine is expected to be driven mainly by the precipitation regime, with the proportion of Aleppo pine increasing toward the driest border and with holm oak being the dominant species in areas with higher precipitation. Changes of dominance of holm oak and Aleppo pine also respond to water availability at the local scale. In this case, variations between species depend on different factors in a complex way, because reduced soil-moisture levels may result either from low precipitation or from topography and edaphic features. The dynamics of holm oak–Aleppo pine forests are also determined by temporal changes in canopy closure; that is, forest recovery after disturbance. In this case, the proportion of Aleppo pine would increase in recently disturbed stands (i.e., with high light intensity reaching the forest floor), whereas regeneration of holm oak would be dominant under partially closed canopies.

Theories of forest dynamics developed in humid regions may apply only poorly to Mediterranean plant communities, where vegetation change is qualitatively or quantitatively different. Thus, succession in temperate forests appears to be driven by differences in light availability and shade tolerance; but in Mediterranean plant communities, water limitation is of greater importance for the distribution of forest species. In Mediterranean landscapes the interaction of life-history strategies with changing environments is difficult to infer from observational and experimental studies. A mechanistic approach, in which competition or plant performance is measured as a function of resource availability, seems more feasible. The idea should be to develop multispecies models calibrated specifically for Mediterranean forests in a combined program of modeling, field research, and experimentation.

Resumen

En este trabajo se revisan los aspectos más relevantes en el desarrollo de una teoría ecológica mecanicista sobre la estructura y dinámica de los bosques mediterráneos, en concreto sobre los bosques mixtos de encina (*Quercus ilex* L.), una especie tolerante a la sombra, de crecimiento lento, y que rebrota vigorosamente después de una perturbación, y pino carrasco (*Pinus halepensis* M.), una especie de crecimiento rápido, no rebrotadora, e intolerante a la sombra. Los principales objetivos de este estudio son: introducir algunas de las principales características de estos bosques, mostrando su complejidad estructural y sus peculiaridades históricas; mostrar que gran parte de esta complejidad puede reducirse conceptualmente a dos principales factores de variación, la disponibilidad de agua en el suelo y una compleja interacción de regímenes de gestión y perturbación; y contrastar las características únicas de los sistemas mediterráneos con las de otros sistemas en los que se han basado gran parte de las generalizaciones que se han hecho en ecología.

En las regiones de clima mediterráneo, las plantas deben enfrentarse a diferentes restricciones: limitación hídrica, competencia por la luz, y un conjunto complejo de regímenes de perturbación, principalmente fuego, herbivoría, y explotación humana. La respuesta de las especies a un conjunto de limitaciones ambientales depende de la combinación de caracteres fisiológicos y morfológicos. En los bosques de pino carrasco y encina, el límite inferior de distribución de las especies viene controlado por el estrés hídrico de la estación, mientras que el límite superior viene controlado por la tolerancia a la sombra. Los procesos que generan y mantienen estos patrones están relacionados con las respuestas de ambas especies a lo largo de su ciclo de vida a los ambientes de luz y agua que se generan como resultado de la interacción de los gradientes de perturbación y disponibilidad de recursos.

La dinámica de los bosques mixtos de pino carrasco y encina se puede representar a lo largo de dos principales ejes ambientales: disponibilidad de agua e intensidad de luz; o, lo que es lo mismo, tiempo desde la última perturbación. A una escala regional, la presencia de pino carrasco y encina viene determinada por el régimen de precipitación: el pino carrasco aumenta hacia el extremo más seco, mientras que la encina se hace dominante en áreas con mayor precipitación. A escala local, los cambios en la dominancia de ambas especies también responden a la disponibilidad de agua. En este caso las variaciones entre especies dependen de diferentes factores, ya que los niveles bajos de humedad del suelo pueden ser debidos a la baja precipitación, pero también a la topografía o a las características edáficas. La dinámica de los bosques de pino y encina también depende de los cambios temporales en el cierre de la cubierta, es decir, de la recuperación del bosque después de la perturbación. En este caso, la proporción de pino carrasco se incrementa en los rodales recién perturbados (en los cuales llega mucha luz al suelo del bosque), mientras que la regeneración de encina domina bajo cubiertas parcialmente cerradas.

Las teorías de dinámica forestal desarrolladas en las regiones húmedas se aplican con dificultad en las comunidades de plantas mediterráneas, donde los cambios de la vegetación suelen ser cualitativamente y cuantitativamente distintos. Así, en los bosques templados la sucesión viene determinada por diferencias en la disponibilidad de luz y la tolerancia a la sombra de las diferentes especies, mientras que en las comunidades mediterráneas la limitación hídrica es más importante a la hora de explicar la distribución de las especies forestales. En los ecosistemas mediterráneos, la interacción de las estrategias del ciclo vital con los cambios en el ambiente difícilmente pueden deducirse a partir de estudios observacionales y experimentales. Se requiere una aproximación mecanicista, en la cual la competencia o el éxito de las plantas se pueda medir en función de la disponibilidad de recursos. La idea sería desar-

rollar modelos multiespecíficos calibrados específicamente para los bosques mediterráneos, en los que se combinara la modelización con los estudios de campo y la experimentación.

II. Introduction

Understanding the distribution of plant species is a central issue in plant ecology (Whittaker, 1956; MacArthur, 1972; Crawley, 1986). One of the more established generalizations is that at global and continental scales the distribution of vegetation types is controlled by climate (Braun-Blanquet, 1928; Whittaker, 1975; Woodward, 1987; Stephenson, 1990), whereas at local scales, community distributions are the result of overlapping populations with individualistic distributions (Gleason, 1926; Whittaker, 1956; Horn, 1974; Davis, 1981; Pacala et al., 1996).

Although it has long been recognized that environmental factors and population-level phenomena are important constraints on species performance (e.g., Gleason, 1926; Whittaker, 1975; Harper, 1977) and, more recently, that resource-allocation patterns are important in determining successional positions of species along environmental gradients (Grime, 1979; Tilman, 1988; Smith & Huston, 1989; Pacala et al., 1996), there are surprisingly few studies that directly identify these factors for a particular system, and those that have been conducted usually apply to temperate plant communities (see Tilman, 1982, 1988; Pacala et al., 1996).

Mediterranean-type ecosystems have received increasing attention in recent years (e.g., Kruger et al., 1983; Dell et al., 1986; Tenhunen et al., 1987; Arianoutsou & Groves, 1994; Arroyo et al., eds., 1995; Davis & Richardson, 1995; Moreno & Oechel, 1995). However, the different constraints imposed on the vegetation in these systems, and the resulting trade-offs to cope with them, have not been adequately identified and are still poorly understood. As a result, the main features of these communities have been rarely used to confirm, in some cases, or to contrast, in others, the statements developed for other systems that have inspired generalization in ecology.

In this article we review factors in the development of a mechanistic ecological theory (Schoener, 1986; Tilman, 1990) to account for the structure and dynamics of Mediterranean forests. In particular, we focus our attention on holm oak (*Quercus ilex* L.)–Aleppo pine (*Pinus halepensis* M.) forests, although we also discuss examples from other Mediterranean plant communities.

Holm oak is a shade-tolerant, slow-growing species (Cartan-Son et al., 1992; Mayor & Rodà, 1993) that resprouts vigorously after mechanical disturbance (Ducrey & Toth, 1992; Giovannini et al., 1992) and forms monospecific, well-developed forests. Aleppo pine, in contrast, is a fast-growing, nonresprouting, shade-intolerant species (Panetsos, 1981; Acherar et al., 1984), more tolerant to drought than holm oak (Gil & Prada, 1993; Broncano et al., 1998) that is generally associated with disturbed or xeric sites, where it forms monospecific stands (Gil et al., 1990; Morla, 1993). As a result of both natural trends and human disturbances, pure and mixed stands of both species dominate extensive areas of the Mediterranean region, following a compositional gradient determined by topographic and edaphoclimatic factors and by time since last disturbance.

The main objectives of this report are: to introduce some of the primary features of these forests, showing their structural complexity and historical peculiarities that allow investigation of the effect of anthropogenic activities on ecological processes; to show that much of this complexity can be conceptually reduced to two main factors of variation, soil-moisture gradients and a complex interaction of historical management and disturbance regimes; and

to contrast the unique features of Mediterranean systems with other communities that have inspired generalization in ecology and to show their inherent relevance for theories of community structure. In particular, we will try to reconcile observations and theory that provide the different constraints imposed on the vegetation in this system and the possible resulting trade-offs that plants face.

III. Constraints in Mediterranean Plant Communities: An Evolutionary Perspective

Mediterranean-type ecosystems are defined by a distinctive annual climatic sequence in which a hot, dry summer alternates with a cool to cold, humid period lasting 5–10 months, from fall through winter to spring (Specht & Moll, 1983). The temporal uncoupling of temperature and moisture required for growth conditions, the existence of nutrient-deficient soils, and the occurrence of fire and other disturbances have been major evolutionary forces in shaping these communities (Mooney & Dunn, 1970; Kruger et al., 1983). Although there are several potential evolutionary strategies to surmount a given environmental stress for a given evolutionary history (Jacob, 1977), the number of possibilities becomes limited as the number of stresses is compounded (Mooney & Dunn, 1970). As a result, the vegetation assemblages found in the Mediterranean climates of the world are highly convergent in structure, at least for some traits, regardless of their phylogeny (Mooney & Dunn, 1970; Cody & Mooney, 1978; Cowling & Campbell, 1980; Arroyo et al., 1995). Therefore, life-history traits of Mediterranean plants can be seen as a combination of responses to evolutionary processes driven by the Mediterranean climate, historical effects, and sorting and selective processes acting on pre-Mediterranean lineages (Herrera, 1992). Examples of common adaptations include extensive root systems (Kummerov et al., 1977; Kummerov, 1981; Canadell & Zedler, 1995), evergreen foliage to compensate for nutrient scarcity and to permit year-round production (Chabot & Hicks, 1982; Rundel, 1988; Aerts, 1995), moisture-conserving mechanisms such as leaf sclerophylly (Kummerov, 1973; Rundel, 1988), and traits associated with countering herbivory and fire recurrence, chiefly resprouting (Naveh, 1975; Keeley & Zedler, 1978; James, 1984; Keeley, 1986; López Soria & Castell, 1992). These adaptations have been studied in some detail at the physiological level (Rambal, 1984; Tenhunen et al., 1987; Oliveira et al., 1992; Sala, 1992; Terradas & Savé, 1992; Castell & Terradas, 1994; Castell et al., 1994), but there are few studies that integrate them into a life-history context in order to evaluate their significance at the community level.

Considering this, some of the most integrative traits of Mediterranean plants are their postdisturbance regeneration strategies. These strategies can be described as a continuum, from obligate resprouters, to weak, facultative resprouters, to nonresprouters or obligate seeders (Keeley & Zedler, 1978; Keeley, 1986, 1992). Obligate resprouters can rapidly reestablish their aboveground biomass after disturbance by resprouting from belowground vegetative parts, but they require long, disturbance-free periods for successful establishment of seedlings. Obligate seeders recruit seedlings from soil-stored seeds only in the first years after disturbance but are incapable of vegetative regeneration. Facultative resprouters couple resprouting and seeding in their mode of postdisturbance recovery. These strategies have been basic to the development of the concept of autosuccession (Hanes, 1971), one of the better-established paradigms concerning the dynamics of Mediterranean plant communities. According to this model, Mediterranean communities are resilient to disturbances (sensu Westman, 1986) and suffer temporary structural changes after disturbance but without a significant long-term compositional turnover.

These ideas are widely accepted, but their limits have been little explored (Zedler & Zammitt, 1989), especially in relation to spatial or temporal variability of other ecological factors, including the disturbance regime. According to this, several authors (Keeley, 1986; Stohlgren et al., 1989; Pigott & Pigott, 1993; Bond & van Wilgen, 1996) have suggested that differences in regenerative strategies should be integrated with other vital traits (e.g., longevity, growth rates, or biomass-allocation patterns) and with the response to ecological factors, such as water availability or light intensity, in order to understand the shifts in species dominance observed at larger spatio-temporal scales.

Next we discuss separately the effects of management/disturbance regime and the role of water balance on the population and community ecology of holm oak–Aleppo pine forests. We focus on the effects of these constraints on the establishment of seedlings and the recruitment of saplings and ramets into the canopy, and we outline the resulting effects on the composition of the community.

IV. The Historical Impact of Humans on Forest Composition

No other region in the world has supported a succession and interaction of civilizations like that in the Mediterranean Basin. As a result, one of the most important features of modern plant communities in the Mediterranean region is their anthropogenic structure (Naveh, 1971; Naveh & Whittaker, 1979; di Castri et al., 1981; Ruiz de la Torre, 1985; Blondel & Vigne, 1993). The interaction between human societies and the biota is an issue of growing concern. A combination of exponential human population growth in North Africa and internationalization of the world economy, with a cascade of hierarchical effects at local and regional levels (e.g., agricultural concentration, real estate development, rural exodus) in European countries, is reshaping land-use patterns with more intensity than ever before (Naveh, 1987; Antrop, 1993; Blondel & Aronson, 1995). This makes the Mediterranean region a unique scenario for testing the predictability of ecological theories and for taking responsibility in the development of future human social and economic systems.

Many authors consider present Mediterranean forests as a degenerate form of the original forests after millennia of management, often with overexploitation (Naveh & Dan, 1973; Pons & Quézel, 1985; Ruiz de la Torre, 1990). Human exploitation has nearly driven to extinction some species; others have become dominant because of direct or indirect human activities (Ruiz de la Torre, 1985). The nature of human influence on Mediterranean forests is very varied. It ranges from extensive deforestations, beginning as early as 8000 B.P. (Thirgood, 1981; Pons & Quézel, 1985) to sophisticated multiple-use systems, like the Roman system of ager-saltus-silva, which gave rise to local varieties, like the *dehesa* in Spain or the *montado* in Portugal (Montoya, 1989; Blondel & Aronson, 1995). In general, the interaction of varying land-use practices over several millennia, superimposed on an already heterogeneous environment, has increased diversity both overall and in sites with intermediate disturbance regimes.

Classical works in phytosociology (e.g., Braun-Blanquet, 1936) defended the theory that the climax vegetation in Mediterranean subhumid and humid bioclimates is predominantly evergreen holm oak forest. Over the last decade, data from pollen analyses and from palaeoanthracology have shown that in the northern parts of the Mediterranean Basin and in the mountains of North Africa the establishment of the holm oak (*Quercus ilex*) and cork oak (*Quercus suber*) forests occurred after 6000 B.P., as a result of human impact (Reille & Pons, 1992). Before it was replaced by sclerophyllous oak forest, the dominant vegetation consisted mainly of deciduous *Quercus* (Pons & Reille, 1980). It has been assumed that this inversion of

dominance is due to the fact that over the last few thousand years *Quercus ilex* has been more useful than *Quercus pubescens* (a deciduous oak) to humans, who have consciously or unconsciously favored *Quercus ilex* (Romane et al., 1988).

In regions with a semi-arid cold climate, *Quercus ilex* has a much more continuous record. Pons and Vernet (1971) refer to *Quercus ilex* as the main element of a thermophilous vegetation during the Lateglacial Interstadial and the onset of the Holocene, after the *Pinus* dominance. However, they point out that later human influence could have extended *Quercus ilex* and *Pinus* beyond this climatic region, to the detriment of deciduous *Quercus*.

Recent studies, which infer climatic trends from sources other than vegetation dynamics, question the dominant role of humans in modifying large-scale community composition. These studies suggest that climatic factors (mainly drought) were the primary selective factors in the evolution of community dominance by evergreen sclerophylls (Axelrod, 1975; Beard, 1977; Rundel, 1988) and that anthropogenic effects may have had a much smaller influence than what was previously thought (Pérez-Obiol & Juliá, 1994; Yll et al., 1994).

Concerning Holocene *Quercus-Pinus* dynamics, in northern latitudes temperature fluctuations induced the decrease of *Pinus* and the expansion of mixed hardwood forests (Reille & Pons, 1992), whereas in the southern range, water limitation seems to have been the main element associated with forest dynamics (Pons & Reille, 1980). In the latter, changes in community composition over the last 12,000 years are consistently characterized by the alternation and codominance of *Quercus* and *Pinus* (Costa et al., 1990; Reille & Pons, 1992; Yll et al., 1995). This codominance has been interpreted as a complex mosaic of pure monospecific stands and patches of mixed species, with decreasing *Pinus* associated with increasing *Quercus* abundance (Costa et al., 1990).

V. The Role of Water Availability in Landscape Patterns of Pine-Oak Abundance

Spatial and temporal availability of water is a prime determinant of plant community structure (Whittaker, 1975; Crawley, 1986). The severity of the Mediterranean climate for plant metabolic processes is apparent when the annual course of the temperature-precipitation regime is examined (Fig. 1). The most favorable time for activity is spring, when temperatures are warm and water availability is high. With the onset of summer, the rise in temperature coupled with low precipitation imposes severe drought, and plants are forced to conserve water, despite reducing their carbon gain. In fall, rain returns and soil moisture is recharged, but temperatures become progressively low and growth is again limited.

In that ecological scenario, all plant demographic processes (e.g., survival, growth, or fecundity) are affected by the availability of soil moisture, and the literature is particularly rich in studies emphasizing the role of water stress as the main factor limiting the distribution and growth of species in all Mediterranean regions of the world (e.g., Miller, 1981; Mooney, 1983). Other environmental factors, such as nutrient availability, have been reported as important determinants for vegetation distribution in Mediterranean-type ecosystems, because deficiencies in nitrogen and phosphorous are common in most Mediterranean soils (Bradbury, 1981; Kruger et al., 1983; Specht & Moll, 1983). Nevertheless, several experimental studies have found that fertilization is effective for holm oak or Aleppo pine growth and production only when it is accompanied by irrigation (see, especially, Cartan-Son et al., 1992; Abril & Diego, 1994; Mayor et al., 1994, for holm oak; and Sardans, 1993, for Aleppo pine).

At the population level, water scarcity is also identified as a critical force controlling the regeneration of most Mediterranean species. Seedlings are more sensitive to drought than are
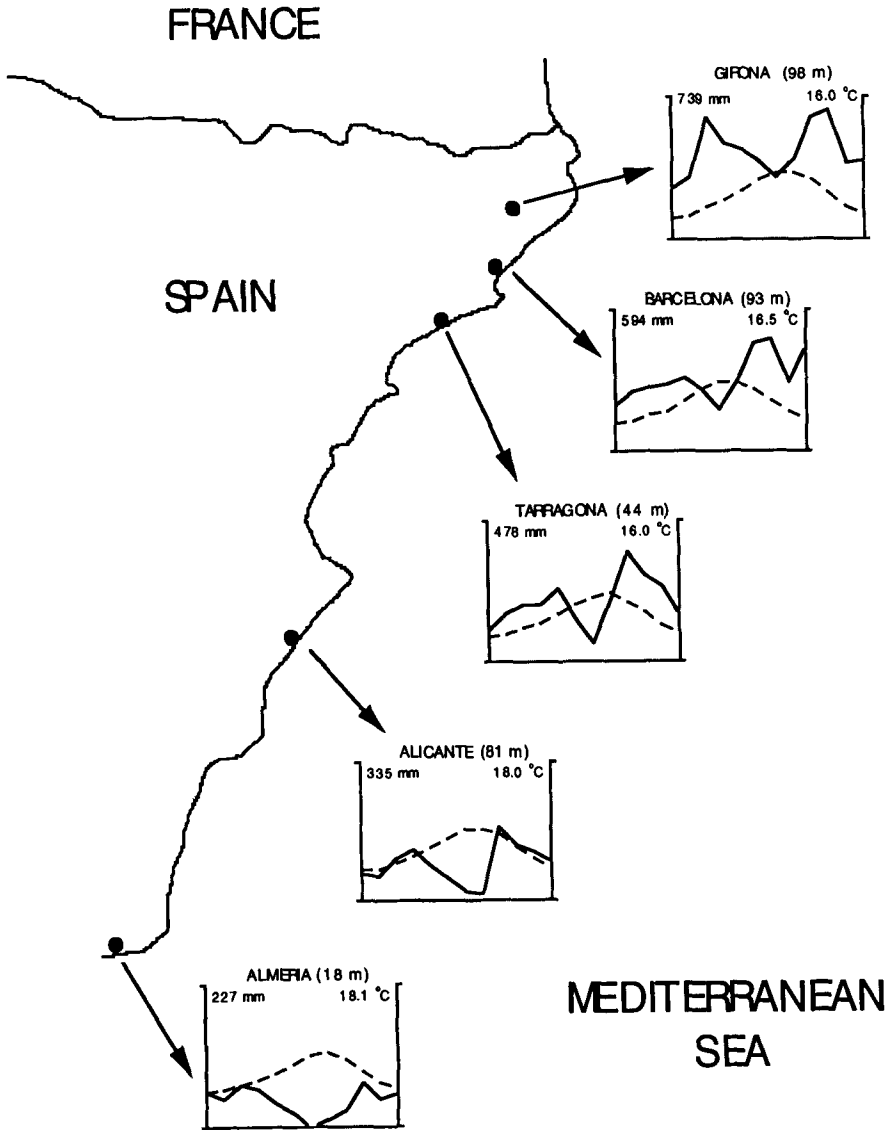
FRANCE

GIRONA (98 m)
739 mm   16.0 °C

SPAIN

BARCELONA (93 m)
594 mm   16.5 °C

TARRAGONA (44 m)
478 mm   16.0 °C

ALICANTE (81 m)
335 mm   18.0 °C

ALMERIA (18 m)
227 mm   18.1 °C

MEDITERRANEAN
SEA

Fig. 1. The mesic-xeric gradient in the eastern part of the Iberian Peninsula. Climatic diagrams (temperature and rainfall) of five meteorological observatories in the north–south gradient are shown. The unbroken line represents rainfall; the broken line, temperature. Elevation (in meters, in brackets), total annual rainfall (in millimeters, left scale), and mean monthly temperature (in degrees Celsius, right scale) are indicated for each observatory.

adult plants because they have not developed yet an extensive root system and/or the capability to close stomata under water stress, both of which are important traits for coping with drought (Oechel, 1988). At this juvenile stage, water stress depends not only on climate and soil capacity but also on the degree of canopy closure above seedlings, their water status improving under partial shade (Bran et al., 1990; Mesleard & Lepart, 1991; Broncano et al., 1998). Thus, studies that deal with the establishment of seedlings and the survival of shrubby species under Mediterranean and semi-arid conditions have stressed the benefits of a partial cover provided by nursery plants during the early phases of seedling recruitment (Callaway & D'Antonio, 1991; Callaway, 1992) or even among adults of different species (Pugnaire et al., 1996). Sensitivity to water stress and tolerance of shade vary among seedlings of different species and have been considered a major determinant of spatial segregation of species in Mediterranean communities (Oechel & Mustafa, 1979; Keeley, 1986; Pigott & Pigott, 1993).

Changes in the composition of holm oak and Aleppo pine stands are observed along a soil moisture gradient in Catalonia, in northeastern Spain, at different scales (Figs. 2, 3). At regional scales, the effect of drought length on the proportion of both species is highly significant (Fig. 2), providing a demonstration of the importance of water in controlling community composition. At the dry end of this gradient (more than 8 months of drought), Aleppo pine forms monospecific stands. In these sites, even the density of pine seedlings decreases from north-to south-facing slopes, following the soil-moisture variations imposed by aspect. At the other extreme of the gradient (fewer than 4 months of drought), holm oak becomes the dominant species. In areas with an intermediate drought length (between 4 and 8 months), mixed holm oak and Aleppo pine are found. In these situations, both species follow a compositional gradient of aspect and altitude (Retana et al., 1996), with higher proportions of pine on south-facing slopes, higher proportions of holm oak on north-facing slopes, and intermediate values for the two species on east- and west-facing slopes (Fig. 3). Concerning altitude, the density and basal area of holm oak increase with elevation, whereas those of Aleppo pine decrease. Consistent with this general trend, and according to the light-moisture trade-off hypothesis developed to explain the distribution of species in other plant communities (see Tilman, 1988), we hypothesize that the distribution of holm oak and Aleppo pine along a soil-moisture gradient would be controlled in the lower part by the effects of dry-season water stress on the performance of seedlings and in the upper part by tolerance of shade.

In the next section we deal with the effects of water and light intensity on the performance of holm oak and Aleppo pine seedlings, as well as with the major morphological and physiological traits involved. The differences between species allow us to characterize the their regeneration niches (sensu Grubb, 1977) in a two-dimensional space defined by light and water availability.

VI. Resource-Allocation Trade-Offs

Plants in Mediterranean-climate regions must face several environmental constraints during their life cycle: water limitation, competition for light, and a complex set of disturbance regimes (mainly fire, herbivory, and human exploitation). The response of co-occurring species to a given set of environmental constraints depends on a combination of physiological and morphological traits, resulting from different phylogenies evolving and being sorted under similar competitive environments (Mooney & Dunn, 1970; Cody & Mooney, 1978; Orians & Paine, 1983). In this section, we discuss which dimensions may be required to characterize the dynamics of mixed holm oak–Aleppo pine forests, and from these considera-
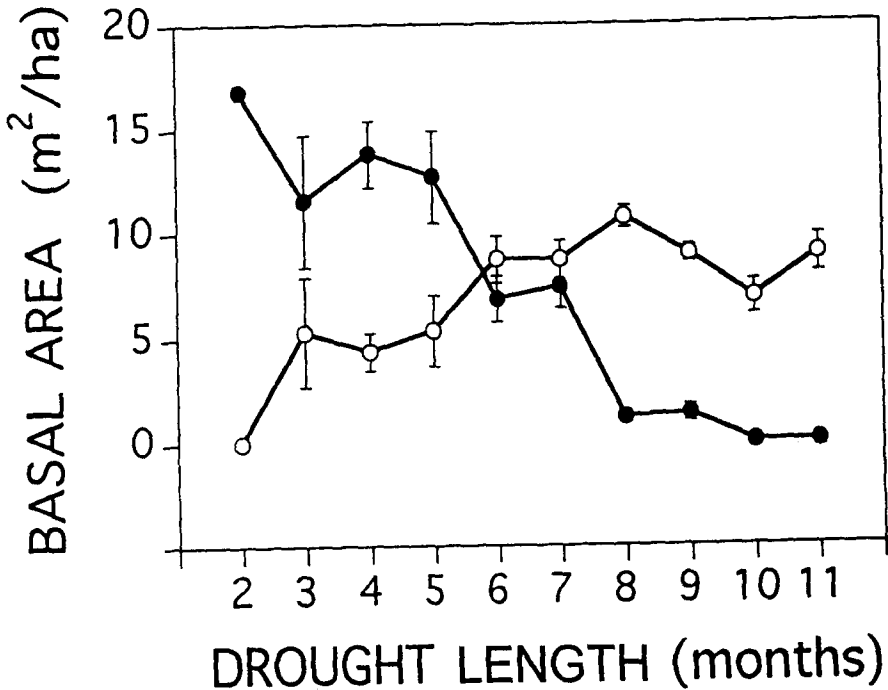
Fig. 2. The effect of drought length on the proportion of holm oak and Aleppo pine at a regional scale. Basal areas (mean ± SE, in m²/ha) of holm oak (black dots) and Aleppo pine (white dots) in Catalonia, northeastern Spain, are shown according to total drought length (in months).

tions we derive a set of assumptions that are central to a theoretical understanding of the dynamics of Mediterranean plant communities.

A. SHADE TOLERANCE VERSUS DROUGHT TOLERANCE

Some authors have suggested that the mechanisms controlling the distribution of plant species along environmental gradients involve resource-allocation trade-offs (Tilman, 1988; Smith & Huston, 1989). For example, costs associated with those traits that enhance growth or survivorship in low-light environments (e.g., biomass partitioning patterns) could affect water-stress tolerance and vice versa (Hirose, 1987; Tilman, 1988, 1990; Smith & Huston, 1989).

The patterns of water and light allocation in holm oak and Aleppo pine seedlings, according to water and light availability, as well as other ecophysiological traits and seedling overall performance, have been extensively studied by Espelta (1996) under controlled conditions. His experiment included five levels of each of the two factors, simulating the broad gradient of precipitation found across the geographical range occupied by holm oak and Aleppo pine, and progressive stages of forest canopy closure. According to Figure 4 (see also Retana et al., 1999), survival of holm oak seedlings decreased with high incident radiation levels and low water availability. Throughout the canopy-closure gradient, the intermediate light level (36 percent photosynthetic active radiation, or PAR) acted as a breakdown point between low radiation levels with high survival and high levels with poor survival. Concerning water avail-
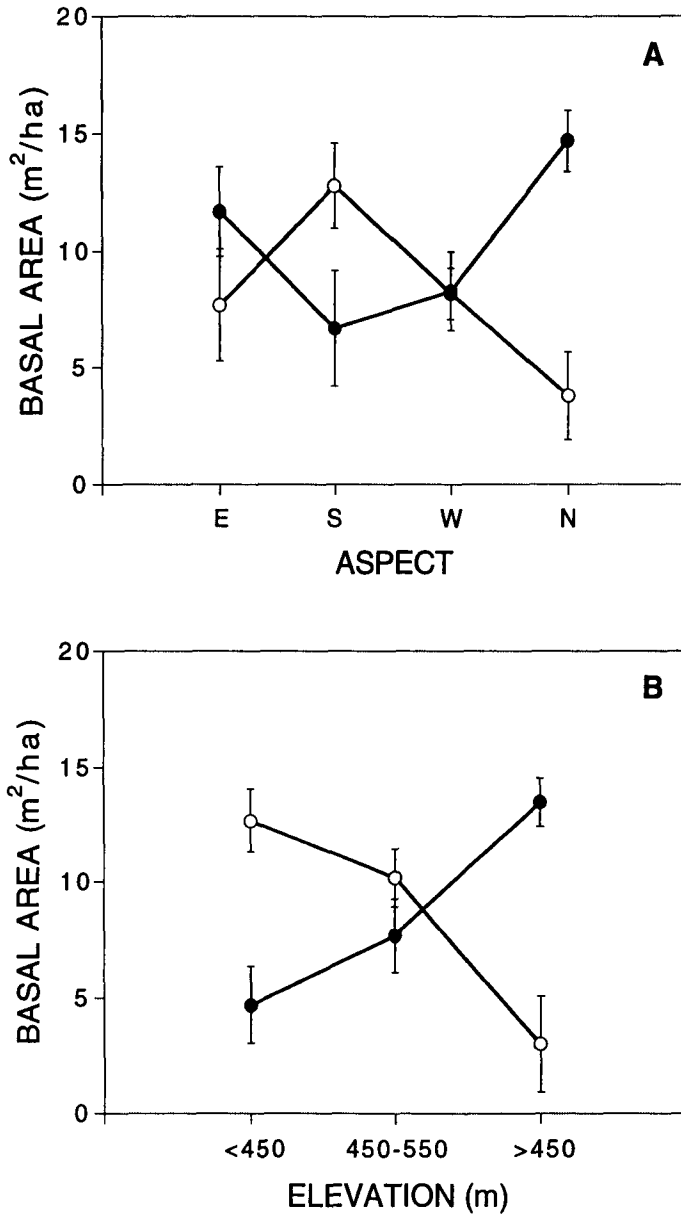
Fig. 3. The distribution of holm oak and Aleppo pine at a local scale. Basal areas (mean ± SE, in m²/ha) of holm oak (black dots) and Aleppo pine (white dots) at the Montseny massif in Catalonia, in northeastern Spain, are represented A) according to aspect, and B) according to elevation.
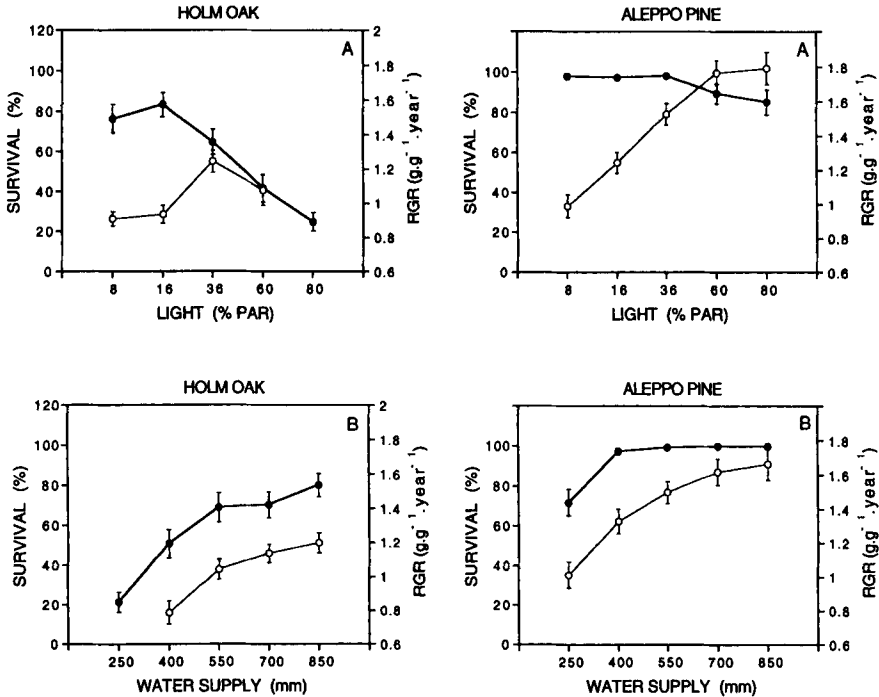
Fig. 4. Patterns of survival (black dots = percentage) and growth (white dots = RGR, in g g-1 yr-1) of holm oak and Aleppo pine seedlings, according to A) light, and B) water availability. The light scale shows the percentage of photosynthetic active radiation (PAR) at which seedlings were grown. The water scale shows the total annual water supply received by seedlings (in mm).

ability, differences between light levels narrowed above 550 l.m-2.yr-1. In contrast, survival of Aleppo pine seedlings was high for all light levels despite differing water availability (Fig. 4). Only among those seedlings receiving the highest light level (80 percent PAR) and the lowest water availability (250 l.m-2.yr-1), was survival clearly reduced, though it remained above 40 percent.

To achieve a more complete view of the range of conditions adequate for seedlings to reach the sapling stage, growth of seedlings under the same light and water levels is also shown in Figure 4. Growth of holm oak seedlings was enhanced by both light and water availability, although no further increase was obtained beyond the intermediate level of light (36 percent PAR). In fact, for most water treatments (excepting 850 l.m-2.yr-1), seedlings attained their maximum growth at an intermediate radiation level, with decreasing values at higher levels. For Aleppo pines, growth increased with both light and water availability, and maximum values were obtained above 60 percent PAR and 700 l.m-2.yr-1.

The integration of survival and growth describes in a more precise way the set of environmental conditions that each species needs in order to reach the sapling stage. Differences between species may be associated with the typical response shown by a shade-tolerant species (holm oak) and a light-dependent one (Aleppo pine) (Canham, 1989; Lorimer, 1989; Kobe et al., 1993; Bazzaz & Wayne, 1994).

Holm oak behaves as a shade tolerant, sensitive-to-water-stress species. Its survival increases under low light levels (see also Broncano et al., 1998), but seedlings, once established, require intermediate light levels to grow and to reach the sapling stage (Espelta et al., 1995). This is a typical response also exhibited by other Mediterranean resprouters (Keeley, 1992) and by *Quercus* in temperate forests (Kolb et al., 1990; Crow, 1992; Kobe et al., 1993).

On the other hand, the high survival of Aleppo pine seedlings receiving low light contradicts, at least during the early establishment phase, the classification of this species as a shade-intolerant one. However, these results agree with those given by Broncano et al. (1998) for recently germinated Aleppo pines and follow the pattern observed for other light-dependent species (Ellsworth & Reich, 1992; Kitajima, 1994). In that sense, the decrease of Aleppo pine growth at low light levels would show that its poor community performance under a closed canopy may be the result of its shade intolerance as a sapling. Light requirements for a given species can change during its life cycle (Augspurger, 1984), especially in the case of conifers, due to the appearance of secondary needles, which may have very different physiological requirements (Whitehead & Teskey, 1995).

A wide array of morphological and physiological traits can be responsible for conferring drought resistance or shade tolerance in plants (Bradford & Hsiao, 1982; Givnish, 1988; Kitajima, 1994). As mentioned above, the tolerance to one of these two limiting factors may result in costs of less tolerance to other limiting factors. Table I summarizes the most important morphological and physiological traits of holm oak and Aleppo pine seedlings.

The lower drought tolerance of holm oak seedlings (resprouter) as compared with Aleppo pine (seeder) agrees with comparative patterns of seedling mortality between resprouters and seeders observed in other communities (Zammit & Westoby, 1987; Thomas & Davis, 1989) and could be related to their biomass-partitioning model between roots, stems, and leaves. In holm oak, as in other Mediterranean species (see Matsuda & McBride, 1986, for oaks in California; and Pate et al., 1990, for resprouters in southwestern Australia), this model develops soon after germination and is characterized by the large amount of resources devoted to roots, even in low-light environments (Broncano et al., 1998). Therefore, a decrease in holm oak survivorship at low water levels could be related to the unfavorable carbon balance derived from the metabolic costs associated with the production and maintenance of an extensive root system.

Nevertheless, a large investment in roots is not necessarily linked to a drought-avoidance strategy. For example, it can be related to seed size (Ledig & Perry, 1966), belowground storage (Tilman, 1988; Pate et al., 1990), or adaptation to nutrient-poor environments (Tilman, 1988), or it may even be the result of natural selection through multiple factors (Hirose, 1987). Moreover, mechanisms associated with drought resistance in seedlings may be also associated with differences in the ability to conserve water that are independent of biomass allocation (Barton & Teeri, 1993). In general, water stress kills very young seedlings by causing a collapse in plant water potential rather than by long-term effects on carbon gain (Barton, 1993). Following this idea, it is important to remark on the results shown by Retana et al. (1999) concerning the poor control of stomatal conductance and the lack of a partial leaf shedding in holm oak seedlings faced with water stress. Thus, the overall results shown in Table I for holm oak seedlings agree with several studies which concluded that holm oak physiology does not show the typical features of a species that has evolved under a Mediterranean climate (Tetriach, 1993).

In contrast, Aleppo pine seedlings present a lower root-to-shoot ratio, with most of their biomass allocated to leaves. However, their water status could be compensated by their higher water-loss control through stomatal closure and the partial shedding of leaves during the summer (Larcher et al., 1981; Bradford & Hsiao, 1982).

Table I

Selected morphological and ecophysiological traits of holm oak
and Aleppo pine seedlings. These traits are among those
that are commonly related to shade tolerance and
drought resistance in plants.

Trait	Holm oak	Aleppo pine
Root-to-shoot ratio	High	Low
Root-weight ratio	High	Low
Leaf-weight ratio	Low	High
Stem-weight ratio	High	Low
Leaf shedding	No	Yes
Stomatal conductance control	Poor	High
Maximum photosynthetic rate	Low	High
Compensation point	Low	High

In addition to their importance to overcome water stress, biomass allocation patterns and leaf turnover have a major influence on growth rates (Bongers & Popma, 1990; Poorter & Lambers, 1991). In Aleppo pine seedlings, a small root-to-shoot ratio, coupled with a fast leaf turnover, may be responsible for enhanced growth under high light, whereas the high root-to–shoot ratio exhibited by holm oak seedlings involves high maintenance costs and determines slow overall growth rates that are poorly ameliorated by light.

B. SEEDING VERSUS RESPROUTING

The trade-off between the use of light and soil resources (such as soil moisture) predicted by Tilman's ALLOCATE model (1988) rests on the assumption that decreasing soil resources favor increased allocation to roots and decreased allocation to stems and leaves. According to the light-moisture trade-off hypothesis (Tilman, 1988), in holm oak–Aleppo pine forests, the lower limit of the distribution of species along a soil-moisture gradient appears to be controlled by dry-season water stress acting on seedling performance, whereas the upper limit seems to be controlled by shade tolerance relative to competitors (Retana et al., 1996). Though with a reduced number of species, these results agree with those observed in other Mediterranean plant communities, where disturbance recruiters (seeders) occupy the lower parts of a soil-moisture gradient and disturbance persisters (resprouters) dominate mesic sites in disturbance-free periods (Specht, 1981; Keeley, 1992; Smith et al., 1992).

When these findings are contrasted with information about species-allocation patterns, we find that Aleppo pine seedlings exhibit low root-to-shoot ratios, whereas holm oak seedlings and adults devote a significant amount of resources to underground structures in all kinds of environments (Canadell & Rodá, 1991; Broncano et al., 1998; Retana et al., 1999). Evidence relating to the model of biomass partitioning for holm oak and other Mediterranean resprouters (Pate et al., 1990; Retana et al., 1999) in light of their drought sensitivity with respect to seeders (e.g. Specht, 1981; Keeley, 1986; Zammit & Westoby, 1987; Thomas & Davis, 1989; Smith et al., 1992) seems to contradict the allocation trade-off hypothesis. This disagreement between observation and theory indicates the need to incorporate disturbance-related trade-offs to models that connect plant traits, species distributions, and community structure.

In general, plant species, or individuals within a species, that grow in environments with limited water and nutrients are expected to have higher root-to-shoot ratios than are those that grow in high-nutrient and/or low-light habitats (Mooney, 1972; Grime, 1979; Chapin, 1980; Tilman, 1988). Accordingly, in Mediterranean forests, differences in root-to-shoot ratios and root depth among oaks seem to explain relative—between and within—species positions along soil-moisture gradients (Matsuda et al., 1989; Callaway, 1990; Canadell & Rodá, 1991) and soil moisture partition among coexisting species (Zwieniecki & Newton, 1994; Wang et al., 1995). However the root-to-shoot ratio may be only an approximate index of allocation pattern for the acquisition of belowground versus aboveground resources for species in which roots serve as storage organs of carbohydrates, nutrients, or meristematic tissue (Tilman, 1988). In Mediterranean forests and forests that are frequently disturbed by fire, herbivory, droughts, or coppicing, many resprouters exhibit large root-to-shoot ratios because of the appearance of belowground woody structures not necessarily related to water uptake (Kummerov, 1981; Rapp & Loissant, 1981; Canadell & Rodá, 1991). Although the adaptive and functional significance of these structures is not well understood (James, 1984; Canadell & Zedler, 1995), up-to-date research suggests a dual function: first as a source of meristematic tissue and second as a storehouse for carbohydrates and nutrient reserves (see the review in Canadell & Zedler, 1995). The first function, the role of lignotubers and burls as a store of concealed buds supporting ramet recruitment after disturbance, is well documented (e.g., Noble, 1984; Hobbs & Mooney, 1985; Stohlgren & Rundel, 1986; Retana et al., 1992), but the functional significance of stored compounds in postdisturbance recovery remains unclear (Chapin et al., 1990).

The ability to resprout can appear as early as the seedling stage and can be under genetic control (Mullet & Bamber, 1978; Noble, 1984). Juvenile resprouters can exhibit a root-to-shoot ratio more than four times greater than that of comparably aged, cohabiting obligate seeder species (Pate et al., 1990). This is the case despite their less extensive lateral root system and is mainly the result of a thickened taproot or lignotuber with high carbohydrate levels (Pate et al., 1990).

Theoretical studies have indicated the community-level significance of postdisturbance regeneration strategies in plant communities (Keeley, 1986; Clark, 1991; Cain et al., 1995; Harada & Iwasa, 1995). Historical and empirical studies have also suggested that differential ability to overcome natural or anthropogenic disturbance may shift species distributions along environmental gradients (e.g., Abrams & Nowacki, 1992; Barbero et al., 1992; Barton, 1993). However, although the postdisturbance regeneration strategies of Mediterranean plant species are well described (e.g., Naveh, 1975; Gill, 1981; Trabaud, 1984; Keeley, 1986; Le Maitre et al., 1992; Bond & van Wilgen, 1996), they have not been integrated with other physiological traits, and therefore it is difficult to interpret community structure and composition at spatiotemporal scales involving resource heterogeneity and variable disturbance regimes.

The vegetation syndromes that characterize the obligate resprouter and seeder strategies of the dominant evergreen shrubs in California chaparral have been reviewed by Keeley (1986) (Table II). In general, fire-persisting shrubs (resprouters) are more sensitive to water stress than are fire-recruiting shrubs (seeders), whereas in turn, and according to the light-water trade-off hypothesis, resprouters are more tolerant of shade than are fire recruiters. As a result, as in other Mediterranean-type plant communities, in the absence of disturbance, resprouters tend to dominate mesic sites, and fire recruiters occupy arid, open sites (Specht, 1981; Keeley, 1992; Smith et al., 1992). The allocation patterns of resprouters versus seeders, and the fact that both strategies (seeders and resprouters) are well represented in most Mediterranean communities, suggests that the costs of forming and maintaining storage-related structures must be substantial (Keeley, 1986; Chapin et al., 1990) and may therefore result in

Table II

Syndromes of the obligate resprouter and obligate seeder of the dominant
evergreen shrubs in California chaparral

Trait	Sprouters	Seeders
	Development	
Safe sites	Deep soil, fissures	Gaps between sprouters
Drought tolerance	Low	High
Growth rate	Low-moderate	High
Shade tolerance	High	Low
Longevity of adults	Very great	Moderate
Longevity of seeds	None	Very great
	Demography	
Distribution of safe sites	Patches	Widespread after fire
Dispersal	High potential	Low potential
Recruitment of seedlings	Under canopy	In fire-created gaps
Population expansion	In the absence of fire	After fire

Source: Reprinted from Keeley, 1986.

tolerance to other factors (e.g., water-stress tolerance, relative growth rate, or reproductive potential). Consequently, as is the case for other communities with an evolutionary history of recurrent disturbances, we follow Barton's suggestion (1993) that trade-offs associated with disturbance-related strategies should be included in models that interpret species distributions in terms of resource-allocation patterns.

VII. A Physiologically Based Succession Model to Describe Landscape Patterns

In the previous sections we reviewed the most relevant determinants of the composition and structure of holm oak–Aleppo pine forests. We suggested that the processes that maintain and generate these patterns are related to the responses of the two species during their life cycle to the water and light environments resulting from interacting gradients of disturbance and resource availability. In this section we summarize the variation of Mediterranean forests structure along these gradients, and we derive the minimum set of assumptions that should be taken into account in order to develop mechanistic models of stand dynamics.

Plant communities can be described as interacting species populations (Gleason, 1926). Therefore, a main goal is to understand community structure and dynamics based on the different life histories and population biology of the components (Horn, 1974; Harper, 1977; Silvertown, 1982; Pacala et al., 1996). Ecologists have long been motivated by the need to relate organismal variation to community structure and dynamics (MacArthur & Wilson, 1967; Horn, 1971; Grime, 1974; Noble & Slatyer, 1980; Strauss & Ledig, 1985; Tilman, 1988). These studies have searched for phenomenological descriptions of species strategies that encapsulate all of the underlying complexity in interpretable parameters—for example, "vital attributes" (Noble & Slatyer, 1980) or organismal allocation tradeoffs (Tilman, 1988). The fact that assemblages of plants with very different evolutionary histories have converged in structure and dynamics when facing similar environmental constraints suggests that some underlying general principles may be responsible for the observed common patterns (Mooney & Dunn, 1970; Orians & Solbrig, 1977; Tilman, 1988).

Despite their simplicity, mechanistic models that describe community structure along resource gradients in terms of resource-allocation efforts seem to explain a wide range of phenomena (Tilman, 1988). Given the specific constraints imposed on vegetation in Mediterranean regions, the trade-offs that organisms exhibit can be significantly different from those of temperate plant communities. Nevertheless, it seems necessary to reconcile these singularities with the fundamental assumptions of more general theories. In turn, integrating postdisturbance regeneration strategies of Mediterranean plants with patterns of resource allocation in models that link species traits with community structure and dynamics may allow us to extend the view of autosuccessional dynamics to broader spatial and temporal scales.

Keeley (1986, 1991, 1992) suggested that the composition and dynamics of chaparral can be characterized by a shifting mosaic of obligate seeders and resprouters through fire regimes and environmental gradients. In the long absence of fire, mesic closed communities are dominated by fire-persister shrubs (resprouters; *Quercus, Rhamnus, Prunus, Heteromeles*) at the expense of fire-recruiter shrubs (*Adenostoma, Arctostaphyllos, Ceanothus*), although on arid, open sites fire persisters fare poorly and fire recruiters persist. Opportunities for population expansion increase immediately after fire for fire-recruiter species, but for fire persisters, opportunities for population expansion arise only in the long absence of fire. The vegetation syndromes that characterize the obligate resprouter and obligate seeder strategies of the dominant evergreen shrubs in California chaparral (Table II) (Keeley, 1986) are consistent with those found in mixed holm oak–pine forests, with pines (obligate seeders) dominating postdisturbance conditions and arid sites and holm oak (resprouters) expanding in mesic sites during fire-free intervals. Given the constraints that affect the dynamics of Mediterranean woodlands, and based on the allocation strategies of the two postdisturbance strategies, we have suggested that the structure of holm oak–Aleppo pine forests may be driven by trade-offs between shade and water-stress tolerance, and possibly by disturbance-related trade-offs associated with the development of storage-related organs.

Aleppo pine regenerates with difficulty under its own canopy (Acherar et al., 1984), and it is frequently replaced by holm oak in areas where both species may potentially coexist. Then, and in the absence of external influences, long-term holm oak dominance in most sites is expected to occur (Rivas-Martínez, 1972; Ruiz de la Torre, 1973; Barbero et al., 1992; Morla, 1993). Nevertheless, in recent decades forest management has favored the expansion of pine (Naveh, 1987; Gil et al., 1990), either directly, by reforestation, or indirectly, by management policies that promote pine dominance (e.g., rural exodus and land abandonment, specific silvicultural practices, or modification of fire regimes; Acherar et al., 1984; Trabaud et al., 1985; Moravec, 1990). The result is that, in most areas, there is no sign of short-term replacement of Aleppo pines by holm oaks. On the other hand, in most holm oak forests of the Mediterranean, present conditions of genet density and thinning disfavor the recruitment of holm oak saplings. Immediately after thinning, exposed conditions create a microclimate that is adverse for the germination and establishment of seedlings, and emerging resprouts close the canopy before the sapling stage is achieved (Espelta et al., 1995). In areas where coppiced stands have been abandoned, holm oak seems to be replaced by other species, such as downy oak, thought to be dominant before human interference (Bran et al., 1990; Bacilieri et al., 1994).

Figure 5 summarizes the distribution of holm oak and Aleppo pine along two major environmental axes: water availability (axis I) and light intensity (axis II; namely, canopy disturbance), according to previously reported results for both species (see Espelta et al., 1995; Retana et al., 1996; Broncano et al., 1998). Axis I can be driven by spatial variations; axis II represents temporal changes. At a regional scale (e.g., in the northern Iberian Peninsula) the presence of holm oak and Aleppo pine is expected to be driven mainly by the precipitation re-
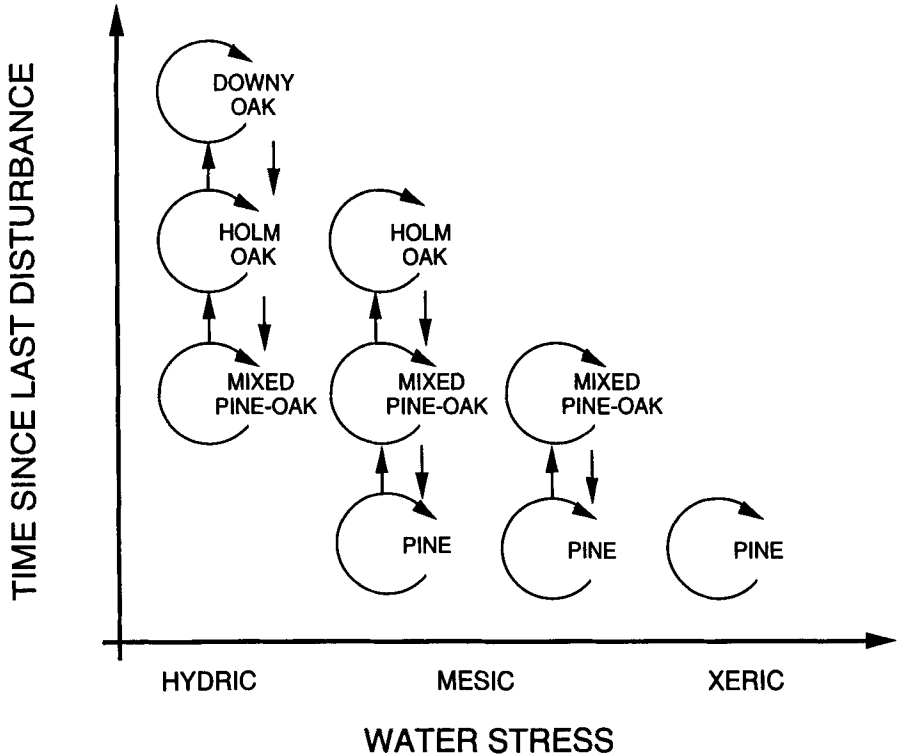
Fig. 5. An idealized representation of transition and dynamics observed in mixed holm oak–Aleppo pine forests. The X axis represents water balance measured as a drought index. The Y axis represents average time since last disturbance (that is, decreasing levels of light reaching the ground). Circular arrows indicate the possibility of autosuccession.

gime (axis I), with the proportion of Aleppo pine increasing toward the driest border and with holm oak being the dominant species in areas with more precipitation. At the upper limit of precipitation, holm oak shares its dominance with other deciduous oaks (e.g., *Quercus pubescens*) and is even replaced by the latter species in the highest-moisture areas (Romane et al., 1988; Bran et al., 1990). Throughout the water-stress gradient, pure holm oak forests are progressively replaced by mixed holm oak–Aleppo pine stands; and those stands, by pure Aleppo pine stands. Beyond this point, drier areas close to the distribution limits of Mediterranean forest, Aleppo pine cannot form true forests, and only scattered individuals are present in typical scrub communities (Chaparro, 1996).

At the local scale, the dominance of holm oak and Aleppo pine also changes in response to the availability of water. In this case, variations between the species depend on different factors in a complex way, because reduced levels of soil moisture may result not only from low precipitation but also from topography, edaphic features, and exposure to wind, among other factors (Gandullo, 1972; Gil et al., 1990; Morla 1993). Thus, on north-facing slopes or in areas with rich soil development (mesic sites), holm oak outcompetes Aleppo pine, and its long-term dominance is expected to occur. On south-facing, xeric sites, the opposite pattern is usually found, with Aleppo pine forming monospecific stands with autosuccessional dynamics.

The dynamics of holm oak–Aleppo pine forests are also determined by temporal changes in canopy closure; that is, forest recovery after disturbance. Axis II in Figure 5 predicts the dominance of each species at a temporal scale, where the presence of holm oak and Aleppo pine is conditioned by the degree of canopy closure due to forest disturbance (mainly thinning, but also fire). In this case, the proportion of Aleppo pine would increase in recently disturbed stands (i.e., with high light intensity reaching the forest floor), whereas the regeneration of holm oak would be dominant under partially closed canopies. Aleppo pine has a light, wind-dispersed seed that germinates well in exposed, stony microsites as well as in sheltered ones (Ruiz de la Torre, 1971; Broncano et al., 1998). This species has a great ability to colonize open areas but is unable to have a successful establishment under its own canopy cover. On the contrary, once holm oak seedlings are established, the best conditions for growth and recruitment into the canopy are met in medium light conditions, where light is not limiting and where environmental extremes (high temperature and water stress) are ameliorated. These conditions are more likely to be found in Aleppo pine monospecific stands or in mixed stands than in holm oak pure stands. The diffuse crowns of Aleppo pines (Ruiz de la Torre, 1971) produce the microclimatic conditions of moderate light interception that holm oak saplings require. Aleppo pines and holm oaks are likely to coexist if the disturbance regime allows the pine to capture openings earlier than oak ramets (given that the oak was already present) or if environmental heterogeneity prevents the holm oak from successfully colonizing available microsites at all times. However, the high mortality rates of low-light-grown pine saplings show that they are usually outcompeted by holm oak in the absence of disturbances. Nevertheless, in the case of holm oak–dominated stands under current thinning regimes, a bottleneck exists at the sapling stage, because holm oak seedlings cannot survive post-thinning conditions (with a sudden increase in light intensity), and only resprouts can recruit into the canopy (Espelta et al., 1995). If the forest remains completely undisturbed, as a result of environmental policies, an effective recruitment of holm oak seedlings would also be uncertain, because they need intermediate light-intensity levels to grow (Retana et al., 1999). In that case, holm oak recruitment would probably require some small-scale disturbances, affecting a few of the individuals on the forest canopy (e.g., episodic dry or snow events or pest diseases), which would create small gaps with intermediate light levels reaching the forest floor but also with a suitable degree of humidity.

It can be hypothesized that the composition of the final stand will depend on the effect of disturbance on two critical stages: seedling recruitment and juvenile or ramet recruitment into the canopy. This effect can be addressed at two levels: that of removal of some individuals from the population (e.g., juveniles killed by fire or adults felled in selective thinning), and that of disturbance of the competitive environment in which the remaining individuals are developing (e.g., long-term thinning or rotation, which creates a bottleneck in holm oak canopy recruitment). Because the result of the interaction of the biological details of the system and the varying levels of disturbance regimes in space and time is far from obvious, mechanistic models are needed in order to give us insight about the different outcomes and the more important parameters that control these processes.

VIII. Predicting Changes in Forest Composition in Response to Changes in Land Use

Since the nineteenth century, the extension of forests has been the dominant trend in Euro-Mediterranean countries. Massive human exodus from rural to urban areas has left the forest

in a sequential mosaic of patches of different ages. The stage of forest development is related to the profitability of firewood versus fossil fuel, to the economy of the timber market, to the frequency of fires, and to environmental demands that result in specific policies like fire exclusion. Under current thinning management regimes, because of the relatively "juvenile" stage of these forests, long-term dynamics are unknown (Romane et al., 1992). For example, the forest may eventually achieve a state of equilibrium based on autosuccession through topographic gradients, or proportions of species may fluctuate according to intensity and frequency of thinning. If these disturbances were to cease, natural disturbance regimes might maintain mixed holm oak–Aleppo pine stands or, on the contrary, drive the system to a shifting mosaic of monospecific patches.

There is little agreement about the ultimate fate of an undisturbed forest. Some authors consider that by the time the Mediterranean climate reached present conditions, humans were already modifying the vegetation, and hence there is no "natural or potential state" as a valid point of reference (Naveh, 1975; Ruiz de la Torre, 1990). For example, theoretically holm oak "climax" forests in southern France and Catalonia are being replaced by deciduous oaks and their associated flora once coppicing ceases (Pons & Vernet, 1971). Even in those sites were holm oaks have been present for extended periods of time, their persistence in the absence of disturbances is questioned. Some authors believe that when undisturbed, the forest enters into a senescent stage similar to the mosaic-cycle model described for temperate regions (Remmert, 1991) or unburned chaparral (Hanes, 1971), which includes self-thinning and weakening by pathogen attacks. This would ultimately lead to oscillation between holm oak and another species, usually a gymnosperm (Schaeffer & Moreau, 1958; Ducrey, 1992). However, it is unclear whether these long, disturbance-free periods are possible, given the genets' remarkable longevity (Barbero, 1988).

At the other extreme, some authors envision preanthropogenic woodlands as perturbation-dependent dissipative structures (Naveh, 1987), or catastrophe-driven systems, with long fire-return intervals and droughts resetting the system to a starting secondary succession (Montoya, 1990). Although land-use patterns have certainly modified the scale of fragmentation and the disturbance regime seen today, this speculative view is concordant with plant life-history strategies (Naveh, 1975; Ruiz de la Torre, 1985), local processes of recruitment (Espelta et al., 1995), palynological records (Costa et al., 1990), and observed dynamics in other Mediterranean plant communities of the world (e.g., Gill, 1981; Zedler, 1981; Kruger & Bigalke, 1984).

The role of disturbances, patchiness, historical events, and human determinants in shaping the structure and dynamics of forests is becoming increasingly appreciated (Spurr, 1954; Biswell, 1972; Whittaker & Levin, 1977; Pickett & White, 1985; Clark, 1991; Herrera, 1992; Ledig, 1992; Blondel & Vigne, 1993). Even in eastern North American and Asian temperate forests, where human determinants have operated at very different scales than in Europe, species distributions reflect a variety of ecological pathways related to water balance, management, and disturbance gradients (Nakagoshi et al., 1987; Abrams & Down, 1990; Abrams, 1992; Clark & Robinson, 1993; Kamada & Nakagoshi, 1993). Therefore, vegetation theories formulated for the Mediterranean region under equilibrium assumptions, which neglect the role of disturbances and of the response of individual species (Braun-Blanquet, 1936; Rivas-Martínez, 1987), are insufficient to adequately characterize these dynamics. Understanding and predicting Mediterranean woodland dynamics along resource and disturbance gradients will require identifying the mechanisms that generate large-scale vegetation patterns, choosing the proper scales of integration to scale up individual species' responses, and recognizing the dynamic nature of these systems.

IX. Conclusions: Challenges for Developing Models of Forest Dynamics for the Mediterranean Region

Mediterranean ecosystems have received considerable attention from botanists, ecologists, foresters, geographers, and other researchers who have developed conceptual models of vegetation dynamics based on their own experiences (Braun-Blanquet, 1928; di Castri et al., 1981; Naveh, 1987; Rivas-Martínez, 1987; Costa et al., 1990; Montoya, 1990; Ruiz de la Torre, 1990; Ducrey, 1992). These studies have highlighted the intrinsic complexity and heterogeneity of Mediterranean systems, casting doubt on the feasibility of developing mechanistic approaches similar to the ones undertaken in better-studied systems. At the opposite extreme, because of the relevance of water stress in Mediterranean climates, plant physiologists and ecologists have invested significant effort in studying the physiological details of some of the most representative species (e.g., Rambal, 1984; Schulze et al., 1987; Tenhunen et al., 1987; Oliveira et al., 1992; Sala, 1992; Terradas & Savé, 1992; Castell & Terradas, 1994; Castell et al., 1994). These studies have tended to focus on parameters with a high intraindividual variability (e.g., leaf-level measurements), so they are not easily related to demographic variables like growth, mortality, or competitive ability or to community-level performance.

Although both types of studies have been extremely useful in increasing our understanding of Mediterranean-type ecosystems, they have also revealed the need to choose the appropriate levels of integration when scaling up ecological processes. Models of forest dynamics appear to be a promising tool for integrating processes taking place at different levels of organization (Shugart, 1984; Horn et al., 1989; Pacala et al., 1996). Malanson & O'Leary (1995) have suggested that a unified Mediterranean-type ecosystem simulator could result from coupling existing physiological models (Tenhunen et al., 1989), the JABOWA–FORET type of stand models (Malanson & O'Leary, 1995), and landscape models (Davis & Michaelsen, 1995). However, Pacala et al. (1996) have warned against the use of models that are not intimately coupled to data (as is the case in the JABOWA–FORET family of models) or too complex to be biologically interpretable, because they can reproduce the observed phenomena even with the wrong mechanisms.

Theories of forest dynamics developed in humid regions may apply only poorly to Mediterranean plant communities, where vegetation change is either less frequent or qualitatively different (Zedler, 1981). For example, temperate forest succession appears to be driven by differences in light availability and shade tolerance (Horn, 1975; Shugart, 1984; Pacala et al., 1996), but in Mediterranean plant communities, characterized by the scarcity of available soil water during the warm season, water limitation is of greater importance for the distribution of forest species (di Castri et al., 1981; Pigott & Pigott, 1993). In holm oak–Aleppo pine forests, water stress during the summer season appears to have a major effect on seedling mortality for both species. Although this effect is much stronger for the holm oak than for the pine, in the drier sites, where the pine forms monospecific forests, water stress still controls the structure of the pine population. The effect of soil moisture is important not only by itself but also because it modifies the sensitivity of species to light. The interaction of moisture and light accounts for the observation that holm oak germination and establishment are achieved mostly in sheltered sites but that, when successfully established in the understory, saplings benefit from medium to high light levels to grow and reach the forest canopy. This characteristic is also important in determining the output of competition between saplings and resprouts in postdisturbance conditions. Aleppo pine, in turn, is a rapid colonizer and is drought tolerant, but it is eliminated under its own cover if environmental conditions allow the persistence of dense stands, and more gen-

erally under holm oak shade. Whereas in holm oak, mortality seems to be concentrated in the germination and seedling stage, sapling mortality seems to be the main factor of density dependence in Aleppo pine populations. The interaction of life-history strategies with changing environments cannot be directly inferred from observational and experimental studies.

Stand dynamics are driven by processes taking place at very short scales (that is, defined by proximate neighbors), which can substantially modify the qualitative output of species interactions (Pacala, 1986) or even ecosystem-level properties (Pacala & Deutshman, 1995). As a result of this "spatial" dimension of plant communities, there may be strong feedback between the spatial and temporal features of the disturbance regime and the vegetation pattern (Minnich 1983; Green, 1989; Moloney & Levin, 1996). In Mediterranean systems, given the scales of the disturbance regimes with respect to those at which species interact, and their postdisturbance strategies, the expected dynamics are qualitatively very different from the ones observed in temperate forests (Zedler, 1981).

In the Mediterranean Basin we only have a slight idea of how anthropogenic regimes may have affected plant community structure in the past (Blondel & Vigne, 1993; Blondel & Aronson, 1995) or of how the new spatial scales of the disturbance regimes associated with present economical conditions will affect vegetation processes (Romane et al., 1992). Thus spatial models seem the main possibility to explore the landscape-level consequences of novel disturbance architectures.

Mediterranean landscapes show a remarkable spatial heterogeneity (Naveh & Lieberman, 1984). Even if this heterogeneity could be reduced to a few factors of variation, it seems prohibitive to calibrate coefficients that describe pairwise species interactions for each combination of factors. Therefore, a mechanistic approach, in which competition or plant performance is measured as a function of resource availability, would seem to be more feasible and interpretable than a phenomenological one, in which competition or plant performance is specified in a set of parameters for each pair of species.

Recent individual-based models of forest dynamics designed for oak–northern hardwoods forests in northeastern North America include some of the features reviewed above (Pacala et al., 1996) and suggest that multispecies models calibrated for other communities may be feasible. Implementing models that are simple enough to be mathematically understandable and that predict and explain community structure and dynamics under different disturbance/management regimes would seem feasible only in a combined program of modeling, field research, and experimentation, all of which consider the natural history of the system under study.

X. Acknowledgments

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