

12 Evolution of life histories in *Pinus*

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'Where soils have been used for some time, have become depleted, and have been given up, pines are known to establish themselves where few other trees can survive' Parsons (1955).

12.1 Introduction

Two extremes may be identified in the study of life histories. One is the traditional approach in which the attributes and patterns of growth and development characteristic of individual species are described and classified. The other is quantitative and reduces life histories to a small set of demographic descriptors, which may be empirically difficult to measure but are logically and mathematically tractable, allowing for generalizations which are hopefully applicable to large groups of organisms (e.g. Stearns 1992). Our approach is mid-way between these extremes, and focuses on synthesizing the multitude of life-history characteristics by describing life-history strategies, which we define as sets of attributes that determine the ecological role of groups of species. Strategies represent an evolutionary compromise to the biotic and abiotic factors that affect the survival and fecundity of individuals and the times and places in which a species can be successful. Grime (1979) proposed a scheme for understanding strategies that emphasizes the trade-offs that are necessary to balance the effect of factors that can be grouped into three major categories: competition, disturbance and stress. Stress, as he defined it, refers to abiotic conditions that limit photosynthetic production and include predominantly nutrient and temperature limitations. Competition, which could be thought of as biotic stress, largely represents limitations to photosynthetic production arising from interference with other species.

Disturbance is the sum of all environmental factors that maintain communities in a state of disequilibrium, e.g. fires, floods, wind, etc. Grime's scheme, though simple relative to the complexity of life histories to be explained, is useful for distinguishing the unique qualities that

separate pines from other groups of woody plants. The first obvious generality is that pines, as with most other conifers, are more tolerant of abiotically stressful sites than angiosperms. Throughout their extensive range they are most abundant where photosynthetic productivity, and therefore competition from other plants, is limited by a lack of resources or by disturbance, or both. This proclivity is shown not only in their natural range, but also by their capacity to prosper and invade in nutrient-limited or disturbed sites far beyond their natural range in the southern hemisphere (Richardson, Williams & Hobbs 1994).

The association of pines and poor soils is almost certainly an ancestral trait, but it may have been reinforced by competition with the emerging angiosperms which were better suited to exploit high-nutrient conditions. Among conifers, including other genera in the Pinaceae (*Abies*, *Picea*, *Tsuga*) as well as more distantly related groups (*Actinostrobus*, *Cupressus*, *Fitzroya*, *Juniperus*, *Taxodium*, *Thuja*), tolerance of poor soils and extreme conditions is the rule. Thus, when the pines radiated in parallel with the angiosperms (Chapters 1 and 3, this volume) – they specialized along ancestral lines. As forest ecosystems developed through the Tertiary, angiosperms came to dominate the most fertile and favourable sites. There seem to be many reasons why this was so. Bond (1989) has pointed out several physiological and developmental advantages of most gymnosperms on infertile sites. As site fertility increases, the net photosynthetic capacity of sclerophyllous-leaved conifers falls significantly below that of broadleaved trees (Reich *et al.* 1995; see also Chap. 15, this volume). Additionally, Hickey & Doyle (1977) point out the potential advantage accorded the newly evolved angiosperms because of the unique highly reticulate venation

pattern and laminate structure, giving them the potential for more rapid growth rates on fertile sites, initially as understory shrubs in low-light environments but later as canopy trees. It is also likely that there was a positive feedback between leaf anatomy/physiology and soil fertility, with angiosperm litter favouring more rapid decomposition, better soil structure, and richer soil biota: a contrast that can be observed today between forests dominated by broadleaved trees and those dominated by pines (Nakane 1994; Aerts 1995).

Although tolerance of low-fertility stress is general among conifers, a capacity to invade and exploit open, disturbed, or early to mid-successional stages of forest development is not; it is in the role of aggressive post-disturbance invaders that pines are most clearly differentiated from other conifers. Many conifers have a considerable capacity to endure in conditions of low light (e.g. *Abies* spp.). Others require the conditions present in old-growth forests for seedling establishment (e.g. *Tsuga* spp.). In contrast, pines have a high light requirement and seedling establishment requires mineral soil or only light litter, and open or slightly shaded conditions (Fowells 1965). Growth rates are generally relatively high, and for some species very high. Conifers like *Cupressus* spp. share with pines the traits of disturbance-related establishment and a high light requirement, but in other respects have a conservative stress-tolerant life history with slower growth rates, and a correspondingly limited invasive capacity with relictual distributions to match.

Fire is the only pre-human disturbance factor that occurs with sufficient frequency and intensity in nearly all climatic zones to be a consistent and strong selective pressure affecting the radiation of pines. We believe that fire and fire effects account for much of the diversity in pine life histories, both for persistence of adults and recruitment of seedlings. Pines have exploited fire-prone environments by modifying their life cycle at different stages, e.g. dispersal, seedling development, adult tolerance and vegetative regeneration (Knight *et al.* 1994). Therefore to understand the diversity of pine life histories it is necessary to explore how fire acts in different regions and different plant communities.

The most fundamental aspects of a fire regime are fire frequency and fire intensity (see also Chap. 11, this volume). Fire frequency, the number of fires per unit time, is largely determined by the rate of fuel accumulation and the number and seasonal distribution of lightning ignitions. Fire frequency becomes a potent selective force when it is at or above levels that produce recurrence intervals shorter than the lifespan of the adult trees. Under these conditions, species that cannot survive the fire either by resisting or by establishing seedlings after fire will quickly be pushed to extinction, and individuals that

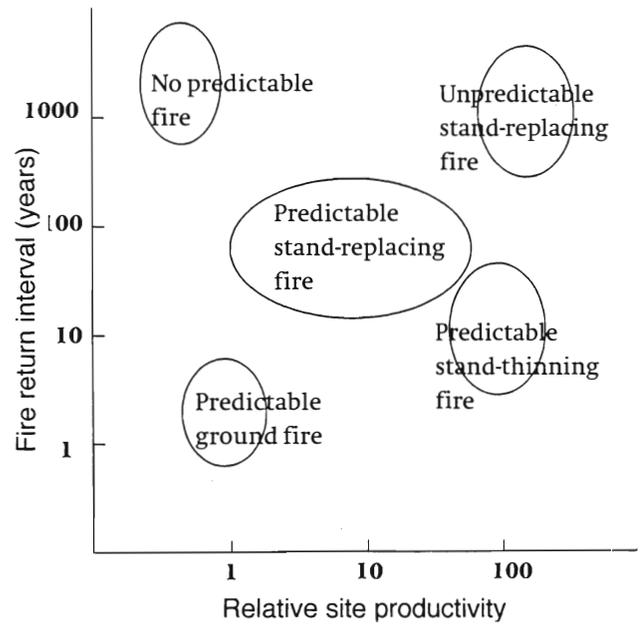


Fig. 12.1. Fire regimes generated by patterns of site productivity and fire recurrence interval.

develop traits that benefit most from fire will leave more offspring. In landscapes of the present and recent past, anthropogenic fire has been common and while it has certainly affected the distribution and abundance of pines in many places (e.g. Denevan 1961; Wang 1961; Chap. 1, this volume), we maintain that it is too recent to have been a major factor in life-history evolution.

Fire intensity, the heat release per unit time and per unit length of a fire, is important because it determines the degree of damage to tissues exposed to the fire and also the likelihood of spread, most importantly the probability that fires will carry into the canopies and propagate through the crowns. It is affected by quantity and structure of fuels and therefore indirectly by fire frequency. It is also sensitive to changes in fuel moisture which generally vary significantly with the seasons. Fire intensity is primarily important in life-history evolution because fire severity limits the adaptive options.

12.2 Ecological strategies in pines

The ecological role of pines may be described as trees specialized for moderate to low-fertility habitats and the exploitation of open conditions imposed by severe limitations on growth, because of aridity and/or cold, or resulting from disturbance. Variations on this basic theme are attributable to evolutionary histories that differed with respect to site productivity, disturbance frequency (fire in particular), and the interactions between them (Fig. 12.1).



Fig. 12.2. *Pinus aristata* on dolomite in the White Mountains, California, USA (photo: J.E. Keeley).

On extreme sites where growing seasons are cut short by low temperatures and aridity, fuel accumulation will rarely be sufficient to sustain fire spread, regardless of ignition frequency, and fire is either absent or too rare to be a significant evolutionary influence. In such situations competitive stress imposed by other woody plants is low but abiotic stress is high. With increased productivity competitive stress would be expected to increase, but this can be nullified or reduced by an increase in the frequency and intensity of fires, which are to be expected with the more rapid and spatially uniform accumulation of biomass. Each landscape will have a unique set of properties that determine rate of fuel accumulation, its size and distribution, the probability of ignition, and the moisture conditions at the time of ignition. These will determine the probability of a site being subjected to (1) stand-replacing crown fires; (2) ground fires that consume understoreys; or (3) stand-thinning fires that burn in a mosaic of ground and crown fire. This will have a profound influence on the evolutionarily stable strategies possible for a given landscape. Here we will relate these patterns of life history to fire regimes across the natural productivity gradient.

12.2.1 Very low site productivity [no predictable fires]

Timberline pines

In western North America, half a dozen pine species occur in timberline forests above altitudes of 2500 m. The most stressful timberline sites are those on the desertic side of the main mountain ranges. Here, biomass production is severely limited by the combination of very short, cool growing seasons and rocky poorly developed soils (Fig. 12.2). Productivity is very low, and therefore fire almost unknown (Fig. 12.1). High winds may be locally important, but are not generally a cause of significant mortality, and thus more of a stress than a disturbance. Species characteristic of these very extreme sites include *P. aristata*

(Colorado bristlecone pine), *P. flexilis* (limber pine) and *P. longaeva* (western bristlecone pine). Growth rates are extremely slow. Wright (1963) reported ages up to 40 years for 'seedlings' less than 15 cm tall. Mature trees are noted for their great longevity. Many individuals are more than 1000 years old, and for *P. longaeva* maximum ages can exceed 4000 years. This remarkable tenacity is thought to be a result of the dramatic reduction in respirational demand, arising from branch and bark die-back, leaving old plants with only a narrow strip of living tissue (Wright 1963; LaMarche 1969). Because of their longevity, seedling establishment in these species can be very low and sporadic without imperilling the population. At one site Billings & Thompson (1957) reported no *P. longaeva* seedlings or saplings less than 10 cm basal diameter and very few less than 30 cm. Wright & Mooney (1965) found that *P. longaeva* seedling establishment is restricted by *Artemisia tridentata* (sagebrush) which shades them out. In the White Mountains of eastern California, *P. longaeva* establishes largely on phosphorus-deficient dolomite soils, which apparently exclude sagebrush but allow the sclerophyllous pines to persist. On the adjacent quartzite soils the pines are eliminated due to competition with sagebrush and lack of tolerance of the more xeric conditions created by the better-drained substrate, a critical factor on these rain shadow sites that receive <350 mm precipitation per year. Thus, lacking periodic disturbances that open up sites, seedling recruitment is restricted to fairly exacting conditions of nutrient-deficient soils in arid ranges; conditions that make seedling establishment precarious and unpredictable.

We interpret the life history of these long-lived trees to be the expected outcome of selection in an environment in which opportunities for establishment are rare, but the capacity to endure is rewarded by the opportunity to establish offspring in circumstances where there is minimal threat of competitive displacement. If theoretical models beginning with Murphy (1968) are to be believed, it is variable juvenile mortality that has been the driving force favouring longevity.

At timberline in more mesic ranges (with annual precipitation 500–1000 mm), enough biomass may accumulate to carry wildfires occasionally and thus some species such as *P. albicaulis* (whitebark pine) and *P. flexilis* may have the opportunity to disperse into burned sites, previously dominated by other conifers (Shankman 1984; Habeck 1987; Tomback 1986; Tomback, Hoffman & Sund 1990). On these sites the pines play a seral role, with higher growth rates and curtailed life spans (Veblen 1986; Morgan & Bunting 1990; Keane & Morgan 1993). As shade-tolerant conifers re-invade such sites, *P. albicaulis* seedling establishment ceases (Fig. 12.3) and the populations survive only in more extreme subalpine sites. On rare occasions, typical

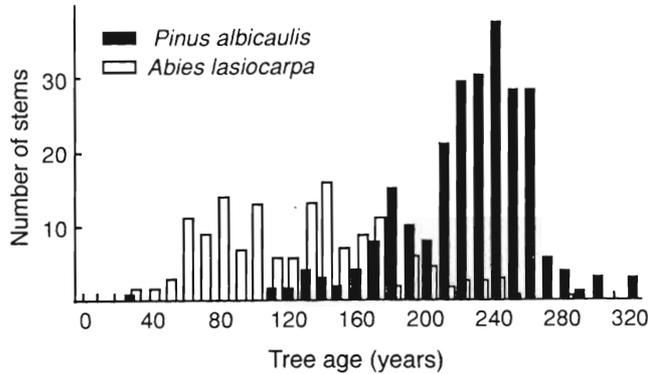


Fig. 12.3. Age distribution for whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*) (redrawn from Morgan & Bunting 1990).

timberline species such as *P. flexilis* occur below 2000 m, but due to greater fire-return intervals, never reach the longevity typical of higher subalpine sites (Schuster *et al.* 1995).

Other timberline species such as the European alpine *P. cembra* (Swiss stone pine), Eurasian boreal *P. sibirica* (Siberian stone pine), Korean *P. koraiensis* (Korean stone pine), and East Asian alpine *P. pumila* (dwarf stone pine) are similar in their persistence on extreme high-elevation/latitude sites, and ability to colonize burned forests (Paryski 1971; Contini & LaVarelo 1982; Lanner 1990). As discussed later, both these Old World and New World subalpine pines depend upon a remarkable coevolution with birds for seed dispersal (see also Chap. 14, this volume), which play a prominent role in the colonization of burned forests.

Desertic pines

The growing season for timberline species is largely limited by low temperatures, but for lower-elevation western North American desert or pinyon pines, the growing season is cut short by both winter cold and summer heat, as well as by severe water deficits. Above-ground seedling growth rates are extremely low, but survival of established trees is high with individuals reaching ages of 400 to > 900 years (Fowells 1965). Seedling establishment is episodic and population age structure is markedly affected by drought (St Andre, Mooney & Wright 1965), which differentially reduces seedling and sapling recruitment more than other age classes (Fig. 12.4). Seedlings survive best in the shade and moisture provided by 'nurse plants' and establishment in the open is rare (Fowells 1965). Consequently, the desertic pines are often relatively shade-tolerant, and can apparently colonize higher elevation closed-canopy pine communities (Barton 1993). Because of their thin bark and lack of self-pruning, however, they are intolerant of fire, which is probably the primary control on their upper elevational distribution.

Within their natural range, biomass accumulation is limited and thus disturbance from fires is infrequent and

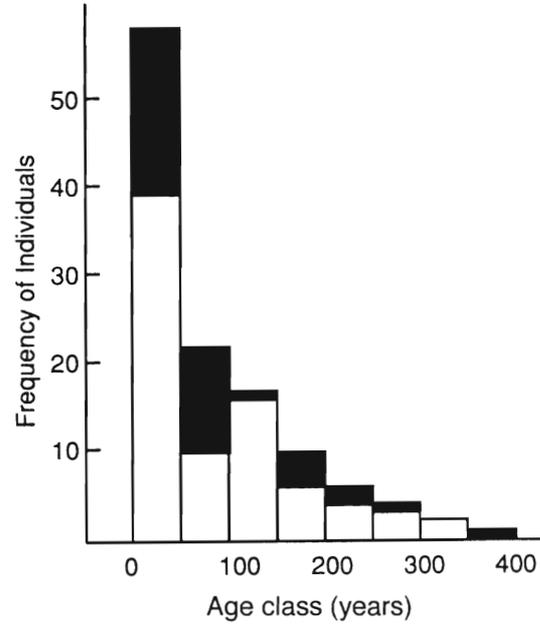


Fig. 12.4. Age distribution for singleleaf pinyon pine (*Pinus monophylla*) affected by severe drought (redrawn from St Andre *et al.* 1965) ■, seedling recruitment; □, sapling recruitment.

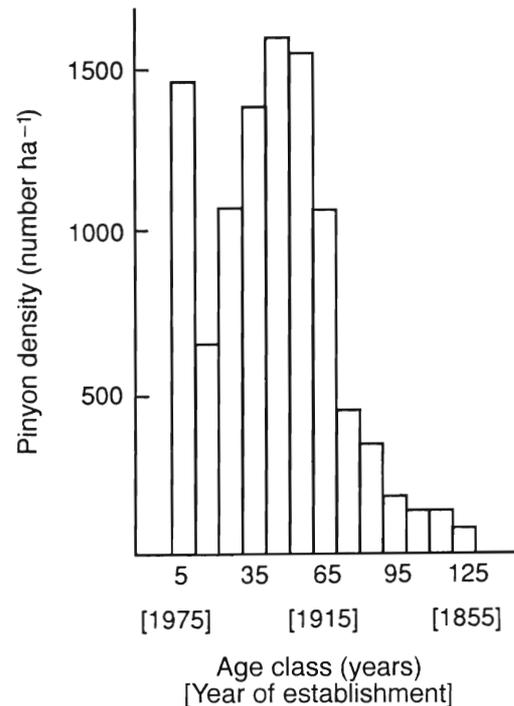


Fig. 12.5. Age distribution for singleleaf pinyon pine (*Pinus monophylla*) recolonizing a site burned in the mid-19th century (redrawn from Tausch & West 1988).

unpredictable, being dependent upon exceptional rainfall years that lead to herbaceous growth sufficient to carry fire. If stands are burned, pinyon pines such as *P. monophylla* (single-needle pinyon) are typically eliminated from the site and invade very slowly (Fig. 12.5) (Barney &

Table 12.1. Distribution of characteristics interpreted as evolutionary adaptations to fire in selected species of pines

<i>Pinus</i> taxa	Grass Stage	Resprouting	Serotiny	Thick Bark	Self-pruning
<i>attenuata</i>	-	-	++++	-	-
<i>banksiana</i>	-	-	++++	-	-
<i>brutia</i>	-	-	++	+	+
<i>canariensis</i>	-	++++	-	+++(+)	-
<i>clausa</i>	-	++++	++++/-	-	-
<i>contorta</i> subsp.					
<i>latifolia</i>	-	-	++++/-	-	-
<i>coulteri</i>	-	-	-/+	++	-
<i>devoniana</i>	++++	-	-	++	++
<i>echinata</i>	-	++++	-	+	+
<i>elliottii</i> var.					
<i>densa</i>	-/+	-	-	++	++
<i>greggii</i>	-	-	++++	+	-
<i>halepensis</i>	-	-	++/-	+++	+
<i>jaliscana</i>	-	-	++++	+++	+++
<i>jeffreyi</i>	-	-	-	++++	++++
<i>lambertiana</i>	-	-	-	++++	++++
<i>leiophylla</i>	-	++++	-/+	+++	+++
<i>merkusii</i>	++++/-	-	-	++	++
<i>montezumae</i>	++++	-	-	+++	+++
<i>muricata</i>	-	-	+++	+++	+
<i>oocarpa</i>	-	++++	++++/-	+	+
<i>palustris</i>	++++	-	-	++	++++
<i>patula</i>	-	-	+++	++	+
<i>ponderosa</i>	-	-	-	++++	++++
<i>pringlei</i>	-	-	-/+	+++	+++
<i>pseudostrobus</i>	-	-	-	+++	++++
<i>pungens</i>	-	+	++++	+	+
<i>radiata</i>	-	-	++	++	+
<i>resinosa</i>	-	-	-	++	+++
<i>rigida</i>	-	++++/-	++/-	++	-
<i>serotina</i>	-	++++	++++	+	-
<i>torreyana</i>	-	-	-/+	+	+
<i>virginiana</i>	-	+	++++	+	-

Fischknecht 1974; Tausch & West 1988). Some pinyons, e.g. *P. cembroides* (Mexican pinyon) appear to be somewhat resistant to occasional fires that may occur once a century or more (Moir 1982).

In summary, the pines of both stressful high-elevation and desert habitats seem to have evolved towards longevity, most probably because the stress of the environment falls most heavily on the youngest and smallest individuals, thus making establishment rare and highly variable. Fire or other disturbances have little impact on mature individuals and the extreme and stressful sites minimize competition from other woody species. Pines adapted to such extreme sites are in the subgenus *Strobus* (soft pines), suggesting that members of this group have an inherent capacity to endure such abiotic stresses.

12.2.2 Low to moderate site productivity [predictable fires]

On sites with sufficient moisture and nutrients to produce a continuous fuel bed, but no more than relatively moderate plant productivity, all pines exhibit life-history characteristics that we interpret as evolutionary

responses to fire (Table 12.1). Most of the species in this conspicuously fire-adapted group are members of the subgenus *Pinus* (hard pines). Ranking of characteristics in Table 12.1 is relative and should be loosely interpreted to indicate importance. Some traits such as serotiny are well developed in some subspecific forms and not in others. Quantitative comparative data on characters such as bark thickness and degree of self-pruning are lacking and these rankings are based on personal observations or inferred from descriptions and photographs in the literature. Limitations are manifold. For example, bark thickness is only one measure of degree of insulation and this character, as well as degree of self-pruning, may have adaptive origins unrelated to fire. The 'grass stage', resprouting, and serotiny characteristics are considered in all instances to be directly selected for by fire. Here we will relate these to patterns of fire regime and site productivity, but see Chap. 11 (this volume) for coverage of community-level responses to fire.

Low to moderately productive sites with high fire frequency [predictable ground fires]

One of the most remarkable life-history traits of any woody plant is exhibited by species of pines at low latitudes in unproductive sites typically on excessively drained sandy soils in warm humid climates with frequent low-intensity ground fires fuelled by a herbaceous understorey. The most studied species in this category is *P. palustris* (longleaf pine), which is widely distributed on relatively unproductive nutrient-poor sandy sites in the coastal plain of the southeastern USA (Christensen 1977). These conditions lead to a sparse canopy cover and establishment of herbaceous wiregrass (*Aristida* spp.) understorey. Despite the high rainfall (>1000 mm yr⁻¹), the sparse canopy results in high soil albedo and rapid drying of fuels. Summer thunderstorms generate the highest frequency of lightning strikes in North America (Komarek 1974), and nearly 60% of the wildfires in the USA occur in this small region (Christensen 1981). On longleaf pine sites the fuel load of the herbaceous understorey is insufficient to generate fires that are much threat to the adult pines, although temperatures are sufficient to kill seedlings and saplings of most species (Chapman 1936; Garren 1943; Landers 1991). In response to these conditions, *P. palustris* has evolved delayed seedling development, whereby internode elongation is depressed for the first five to 20 years of development (Fowells 1965), resulting in seedlings persisting with a bunchgrass growth form (Fig. 12.6). During this grass stage, needles with high fire resistance are produced soon after germination and protect the terminal bud from fire, thus making seedlings extremely resistant to fire (Crocker & Boyer 1975). During the grass stage an extensive root system and carbohydrate stores accumulate



Fig. 12.6. Longleaf pine (*Pinus palustris*) grass stage (photo: J.E. Keeley).

(Pessin 1938; Brown 1964). After many years in the grass stage, seedlings 'bolt' and exhibit rapid internode elongation, resulting in very high growth rates, with as much as 1.5 m growth in three years (Mattoon 1922). During this stage the saplings are susceptible to injury from wildfires (Garren 1943), but become increasingly resistant to fires due to development of moderately thick bark and self-pruning of lower branches. After several decades, trees are quite resistant to fire, and may live for several hundred years (Platt, Evans & Rathbun 1988), unless an absence of fire allows fuels to accumulate and generate fires that can scorch the crowns (Glitzenstein, Platt & Streng 1995).

There can be little doubt that the regime of predictable ground fires has selected for the unusual pattern of seedling/sapling growth, and also permitted and possibly selected for the extreme shade intolerance which makes seedling establishment rare in the vicinity of established adults (Garren 1943; Grace & Platt 1995a). The result is a species dependent on fire and therefore sensitive to changes in fire regime. The greatest threat to the persistence of *P. palustris* is competition from oaks and other hardwoods and fire plays a critical role in reducing oak canopies (Moser 1989; Rebertus, Williamson & Moser 1989; Glitzenstein *et al.* 1995). It has been hypothesized that the needle attributes that produce higher temperatures in pine leaf litter relative to oak litter, have been selected because they enhance sites for pine recruitment (Williamson & Black 1981). This is supported by the observed relationship between proximity to longleaf pines and crown survival of oaks after fire (Fig. 12.7).

Undisturbed systems exist in a dynamic balance between pine density, understorey fuels, competing hardwoods, and fire recurrence. In undisturbed systems, as pine tree density increases, shading and pine leaf litter accumulation increase so that conditions for seedling growth are less favourable and fires are hotter, killing both pine seedlings and hardwoods (Grace & Platt 1995b).

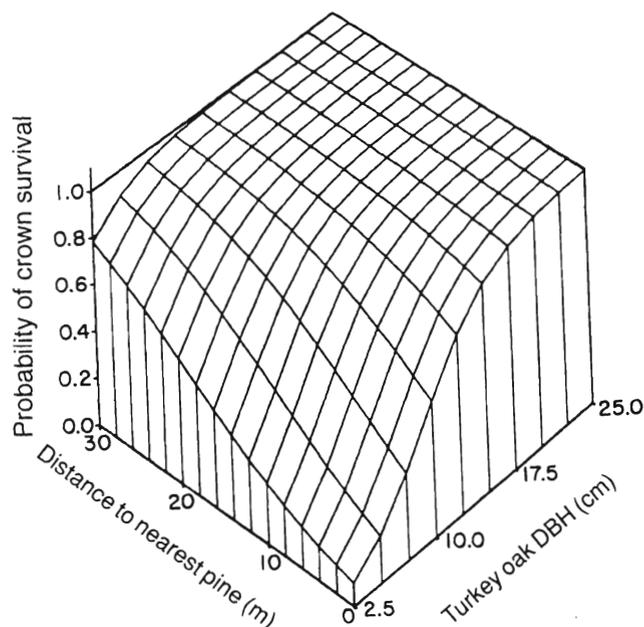


Fig. 12.7. Effect of proximity to longleaf pine on postfire crown survival of oaks (from Rebertus *et al.* 1989).

Patches that appear because of the death of trees are most suitable for recruitment because they will have less intense fires and ample light, leading to recruitment and the ultimate disappearance of the patch. In general high fire frequency stimulates understorey herbaceous fuels which reduce oak and other hardwoods, thus favouring pines (Platt, Glitzenstein & Streng 1991). This balance can be upset by human interference. It has also been hypothesized that anthropogenic removal of longleaf pines has eliminated pyrogenic fuels necessary to sustain frequent light fires (Christensen 1981). When fires are suppressed, recruitment is halted (Fig. 12.8), and stands stagnate (Hartnett & Krofta 1989).

The grass-stage attribute is uncommon in *Pinus*, but it occurs in widely disjunct and distantly related taxa and has undoubtedly evolved more than once. It is a prominent part of the life cycle of *P. merkusii* in Southeast Asia; this is the only species that occurs naturally in the southern hemisphere, ranging from approximately latitude 20° N to 2° S (Mirov 1967). As with *P. palustris*, it is distributed on nutrient-poor and well-drained sandy soils in association with xerophytic dipterocarps and a herbaceous understorey (Turakka, Luukkanen & Bhumibhanon 1982). The relationship of *P. merkusii* to fire is also very similar to that of *P. palustris*. Despite the relatively high annual rainfall (1000–2000 mm), these xeric poorly vegetated sites are susceptible to frequent fires, especially during the hot dry season which may average 37 °C (Koskela, Kuusipalo & Sirikul 1995). Adult trees survive these low-intensity fires due to thick bark and moderate self-pruning (Werner 1993; Koskela *et al.* 1995). Annual fires are often lethal to

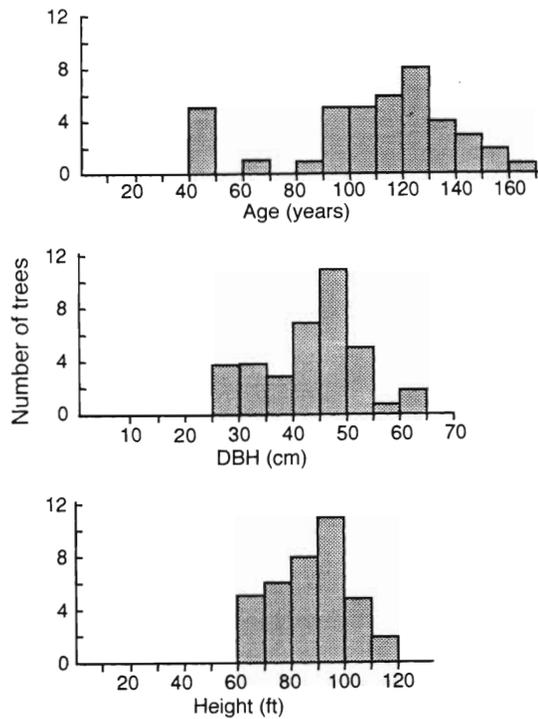


Fig. 12.8. Lack of longleaf pine recruitment on sites protected from fire (redrawn from Hartnett & Krofta 1989).

first-year seedlings, but by the second year of growth *P. merkusii* seedlings develop fire-resistant needles and remain in a grass stage for five years or more. Duration of the grass stage in *P. merkusii* was found to increase with degree of competition (Koskela *et al.* 1995) and the same has been found for *P. palustris* (Brown 1964). Frequent fires and herbaceous fuels maintain fire temperatures at levels tolerable for adult trees as well as the grass-stage seedlings, and reduce competitive inhibition of seedling growth. Koskela *et al.* (1995) proposed that the grass stage was not selected by frequent fires alone, but rather the slow growth rates attainable on xeric sites put seedlings in a state vulnerable to fire for an exceptionally long period. Accumulating carbohydrates during the grass stage allowed rapid growth rates and the potential for rapidly reaching a size that made the sapling immune to fire.

This grass stage also has been reported from several other species (Table 12.1) from similar subtropical oligotrophic sites with high fire frequency (Mirov 1967; Perry 1991). These include a southern Florida variety of *P. elliottii*, the Cuban *P. tropicalis*, and southern Mexican pines (*P. devoniana* and *P. montezumae*). Several of these species, such as *P. merkusii* and *P. elliottii*, exhibit regional variation in presence of the grass stage (Ketcham & Bethune 1963; Mirov 1967; Perry 1991; Koskela *et al.* 1995). Although not well studied, it appears that this grass stage has been selected out of these species in more productive environments, perhaps due to greater fire intensities that make survival of this stage more

tenuous. Although second-year seedlings of *P. pseudostrobus* form a grass-like mound, they do not remain in that stage (Perry 1991; see also Chap. 7, this volume).

Not all subtropical pine species with a regime of predictable ground fires have evolved a grass stage; for example, *P. caribaea* which is common in the llanos of eastern Nicaragua and Honduras (Mirov 1967), lacks the grass stage. One explanation is that the pines are invaders into an anthropogenic landscape from what might have been small original refuges (Parsons 1955) and therefore may not have had time to adapt to the new conditions. But it seems equally likely that the conditions for the evolution of the grass stage may be dependent on a combination of circumstances absent for some species. Some of these may be subtle. For example, the pattern of distribution of fuels may be such that patches exist in which seedling establishment is possible and sapling survival great enough that there is no fitness gain to individuals that have tendencies towards reduced height growth. A constant is, however, that all pines that occur under this regime of predictable low-intensity ground fires have thick bark and extensive self-pruning that ensure adult survival.

Low to moderately productive sites with high-

intensity fires [predictable stand-replacing fires]

With better site conditions, community productivity increases and alters the environment in several important ways. Herbaceous fuels are replaced by woody fuels, and greater water availability means fires are dependent upon unique weather conditions that generate droughts of sufficient duration to dry fuels; thus, fire-return intervals increase (which allows for greater fuel accumulation). These changes lead to an increase in fire intensity sufficient to generate stand-replacing crown fires (Fig. 12.1). Also, as site productivity increases, increased post-fire competition selects for rapid re-establishment, through resprouting and/or serotiny (Table 12.1).

Resprouting pines

In the southeastern USA, as fire intensity increases the grass-stage strategy (as in *P. palustris*) is replaced by the capacity for resprouting from the stem or root collar (Fig. 12.9). Basal resprouting after fire is common in three pines of the eastern USA: *P. echinata* (shortleaf pine), which is best developed on well-drained soils; *P. serotina* (pond pine), which forms extensive stands in poorly-drained depressions; and *P. rigida* (pitch pine), which spans the range of infertile conditions from excessively drained to poorly drained sites (Fowells 1965; Stone & Stone 1954). Seedlings of these three species are vigorous resprouters from axillary buds produced at the base of the stem. Basal sprouting is, however, largely restricted to seedlings and small



Fig. 12.9. Resprouting shortleaf pine (*Pinus echinata*) sapling from southeastern USA (photo: J.E. Keeley).

saplings. Limited ability for basal resprouting is known from a few other species (Table 12.1), including the Mexican–Central American *P. oocarpa* (Ponce 1985). In many of these species, as well as others, e.g. *P. clausa* (sand pine) and *P. canariensis* (Canary Island pine), older saplings and young trees resprout epicormically (Stone & Stone 1943). These preformed buds are well insulated by bark and survive fire in trees up to several decades old (Ledig & Little 1979); they also respond to other disturbances that open the canopy.

It appears that most basal resprouting species are from summer-rainfall climates, which may reflect the increased likelihood of rootstock survival. Another factor could be competition. These sites generally lack post-fire seeding species, but have an abundance of vigorous resprouting broadleaved herbs and shrubs, which may make the sites less favourable for post-fire seeding (Webber 1935; Boerner 1981; Ostertag & Menges 1994). In many woody plants, basal resprouting is commonly interpreted as an adaptation to fire. This assertion has, however, been questioned because sprouting is almost universal in woody angiosperms. It is not, however, the case for conifers where basal

sprouting is rare and therefore much more likely to have been specifically selected by a factor such as fire (Keeley 1981). The resprouting pines all occur on sites of low productivity and high fire frequency, and most also produce serotinous cones (Table 12.1).

Serotinous pines

On infertile sites in a wide range of climates, productivity is reduced to a degree which limits tree height and diameter. Limited height increases the probability that ground fires will carry up into the canopies and smaller diameters make the trees more susceptible to damage or death. The result is that such sites are subject to recurrent intense canopy fires that kill most of the above-ground portion of plants. These frequent uniformly intense fires act to increase even further the uniformity of the tree canopies, providing a positive feedback mechanism for crown fire. Such circumstances offer a clear opportunity for species that tolerate infertility and which thrive in the open conditions that follow fire. It is therefore expected that pine species should be prominent in vegetation of this type. The evolutionary problem the pines faced in adapting to these conditions was how to equip a population of small trees to survive intense fire. The solution was cone serotiny.

In North America, the working definition of cone serotiny is that of Critchfield (1957). He defined a serotinous cone as one that remained closed and on the tree for one or more years after the seeds mature, but could open rapidly when high temperatures melted the resin that seals the cone scales. Lamont *et al.* (1991) considered serotiny more generally and proposed that it be defined as ‘canopy seed storage’ where at least part of the previous seed crop is retained when the current year’s crop of seeds is mature. As will be discussed below, the more general definition of Lamont *et al.* is necessary to encompass the full range of variation in this important life-history trait in pines. The essential feature of serotiny is captured by both definitions: i.e. serotinous species can accumulate seeds, and in the serotinous pines this results in a mass-release of seeds within hours or days after fire. In some species, release can occur at other times. Resin is reported to melt between 45 and 60 °C; on open, xeric sites cones may open on hot summer days without fire (Cameron 1953; Beaufait 1960). Serotinous cones commonly have other features that suggest fire adaptation. Smith (1970) noted that serotinous pines allocate more resources to protective cone structure than to seeds; as a consequence, seeds can survive cone temperatures >200 °C (Beaufait 1960; Knapp & Anderson 1980). In the Californian closed-cone species *P. attenuata* (knobcone pine) and *P. muricata* (bishop pine), and several other serotinous species, the cones not only have thick apophyses but also are strongly reflexed to lie

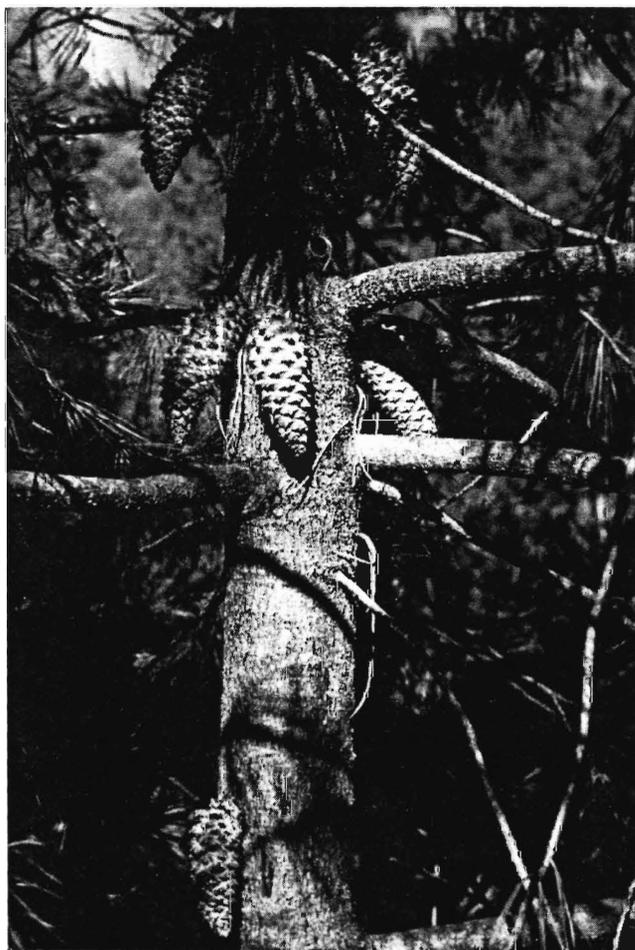


Fig. 12.10. Serotinous cones of knobcone pine (*Pinus attenuata*) (photo: J.E. Keeley).

along the branch. Across serotinous and non-serotinous populations of *P. contorta* var. *latifolia* (lodgepole pine), these traits are indicative of serotiny (Tinker *et al.* 1994). Such traits may minimize radiative and convective heating during fire (however, see the discussion on coevolution).

Serotiny in pines varies among species. At one extreme are the strongly serotinous species such as the Californian *P. attenuata* (Fig. 12.10), in which most of the cone crop remains closed for 15–20 years (Badron 1949; Vogl 1973). At the other extreme are species such as *P. torreyana* (Torrey pine) and *P. coulteri* (Coulter pine) (McMaster & Zedler 1981; Borchert 1985) in which the cones remain on the trees for years but they open at maturity without a heat stimulus. A large proportion of the seeds drop in the first weeks, but some are retained in the proximal portion of the cone and fall over an extended period, possibly in response to scale movement caused by wetting and drying. Similar patterns of cone retention and gradual release of seeds have also been noted for *P. leiophylla* (smooth-leaved pine) and a few other Mexican pines (Perry 1991). Other species such as *P. radiata* (Monterey pine) are intermediate. Their cones

remain closed at maturity but do open without fire after a few years in response to normal temperature extremes or other causes. As a result, their canopies often contain large numbers of open cones.

Serotiny also varies within species. In *P. banksiana* (jack pine), *P. contorta* and *P. rigida* (pitch pine) there is strong circumstantial evidence that serotiny is under relatively simple genetic control, involving perhaps just a single gene that regulates the melting temperature of cone resin (Teich 1970). Ledig & Fryer (1972) concluded that serotinous *P. rigida* were homozygous for the serotiny gene, and heterozygotes at this locus had a mix of serotinous and non-serotinous cones. In light of such a relatively simple genetic control, it is to be expected that this polymorphism could be spatially and temporally quite dynamic.

Indeed, most serotinous pine species are polymorphic for this feature, having populations or subspecific taxa with no closed cones, or polymorphic populations or individuals with both open and closed cones. For example, *P. contorta* is widely distributed throughout the western USA. In the Cascade Mountains of Oregon and Washington, the Sierra Nevada Range of California and Transverse and Peninsular ranges of southern California and adjacent Baja California, var. *murrayana* is uniformly non-serotinous, whereas in the Rocky Mountains var. *latifolia* is often serotinous (Critchfield 1957). These patterns are clearly correlated with differences in site productivity and fire frequency. In the Sierra Nevada, *P. contorta* var. *murrayana* is a subalpine species distributed up to altitudes of 3500 m, in environments characterized by a short growing season, low fuel accumulation, infrequent droughts and low lightning fire incidence (Parker 1986; Sheppard & Lassoie 1985). As is common in other high-elevation pines, *P. contorta* in the Sierra Nevada is quite long-lived (>600 years; Fowells 1965). Also, stands are uneven-aged with seedling recruitment restricted to gaps created by windthrown trees, or to meadows experiencing a drop in water table (Helms & Ratliff 1987) or seedlings may initiate primary succession on granitic outcrops (Rundel 1975; Parker 1986). These lodgepole forests are not replaced by more shade-tolerant species, perhaps due to the shallow granitic soils (Rundel, Parsons & Gordon 1977; Parker & Peet 1984). Where this species co-occurs with more stress-tolerant taxa, e.g. *P. albicaulis*, or less stress-tolerant taxa, e.g. *P. jeffreyi* (Jeffrey pine), forests appear to result from a lottery-type coexistence which derives from infrequent, species-specific pulses of seedling recruitment in response to differing sets of environmental conditions (Carpenter 1991).

In the Rocky Mountains, lodgepole pine may form similar uneven-aged populations on stressful subalpine sites (Despain 1983; Habeck 1987; Johnson & Fryer 1989; Jakubos & Romme 1993). These trees are likewise non-serotinous, and the infrequent fires are patchy enough to

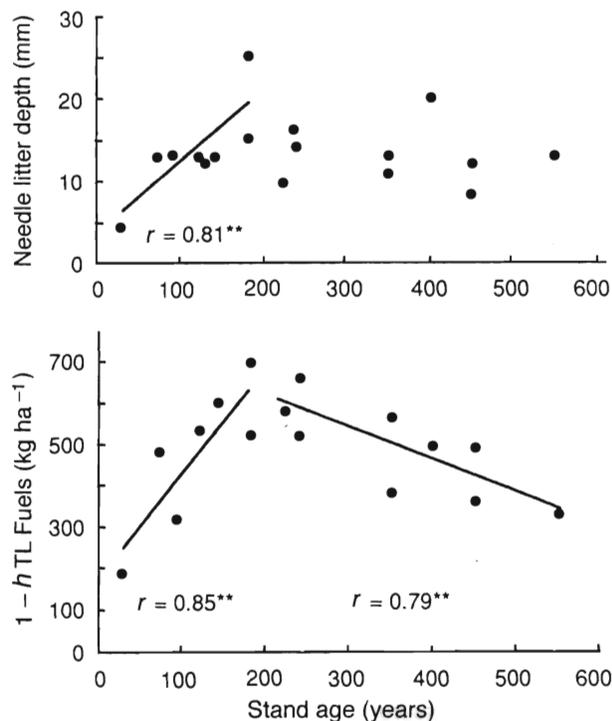


Fig. 12.11. Chronosequence of changes in small fuels capable of supporting ignition and initial fire spread in Rocky Mountain lodgepole pine (*Pinus contorta* subsp. *latifolia*) forests (redrawn from Romme 1982).

leave sufficient seed trees for restocking (Stahelin 1943). More commonly, however, this pine forms dense even-aged stands at lower elevations, down to 1800 m (Arno 1980; Peet 1988). In these situations the longer growing season contributes to a higher growth potential (Rehfeldt 1983, 1987). With higher productivity comes greater fuel accumulation, and with lower elevation a greater probability of summer drought coincident with lightning ignition, a condition that occurs infrequently enough (perhaps only once every few hundred years) that when fires do come they are stand-replacing crown fires (Romme 1982; Muir 1993). On these sites lodgepole pine is generally serotinous, has a shorter lifespan, and in the long absence of fire, can be replaced by more mesic, shade-tolerant *Abies* (fir) and *Picea* (spruce) species (Whipple & Dix 1979; Peet 1988; Tait, Cieszewski & Bella 1988) – successional changes that reduce the potential for stand-replacing fires (Fig. 12.11).

There is evidence that small-scale differences in fire frequency select for genetic differences in populations, and thus frequency of serotiny may reflect local predictability of fire (Lotan 1967; Perry & Lotan 1979). Strongly serotinous species have little to no seed dispersal in the absence of fire and thus are clearly fire-dependent. Serotinous species typically generate dense even-aged stands: for example, Lowery (1984) reported over 400 000 eight-year-old trees per hectare and Fowells (1965) reported nearly 250 000

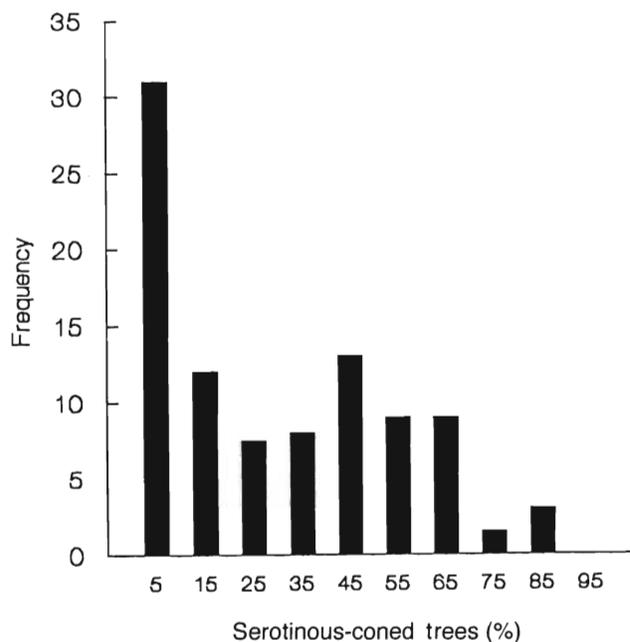


Fig. 12.12. Frequency distribution of serotinous and non-serotinous-coned trees in a Rocky Mountain lodgepole pine stand (redrawn from Perry & Lotan 1979).

trees per hectare at 70 years. Lodgepole pine retains many dead branches, making stands particularly susceptible to stand-replacing crown fires, and raising the possibility that the lack of self-pruning may have evolved to increase pyrogenicity *vis-à-vis* the Mutch Hypothesis (Mutch 1970; Bond & Midgely 1995). While stand-replacing fires are conducive to cone opening (Johnson & Gutsell 1993), and lead to reduced competition from more shade-tolerant species, very intense fires may reduce post-fire seedling recruitment (Ellis *et al.* 1994).

In the Rocky Mountains *P. contorta* var. *latifolia* is typified by mixed populations of serotinous and non-serotinous trees (Fig. 12.12). Despite the widespread occurrence of serotiny throughout its range, the open-cone phenotype remains high, suggesting fires are unpredictable and variable in time and space (Perry & Lotan 1979). Detailed studies of geographical variation in the Rocky Mountains showed that percentage serotiny in a population was not correlated with any environmental variables such as elevation, slope aspect or incline, and topographic position (Muir & Lotan 1985). Following fire, percentage serotiny has been shown to be a more important predictor of seedling density than aspect, inclination, or soil type (Tinker *et al.* 1994).

A similar pattern of serotinous and non-serotinous populations is observed in *P. rigida* in the eastern USA. On the well-drained sandy New Jersey Pine Barrens, populations are uniformly serotinous, whereas elsewhere this character declines along a cline of increasing forest productivity. Ledig & Fryer (1972) maintained that this cline

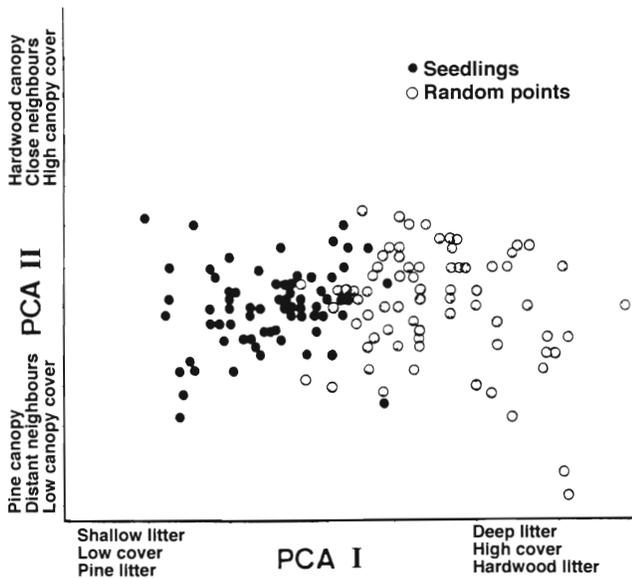


Fig. 12.13. **Principal components affecting Table Mountain pine (*Pinus pungens*) recruitment compared with distribution of random points (from Williams & Johnson 1992).**

was established and maintained by fire occurrence and gene flow. Givnish (1981) doubted the presence of such a cline and thus the importance of gene flow; rather, he provided evidence that serotinous populations were largely maintained by active selection from frequent stand-replacing fires. As site productivity increases, fuel moisture conditions reduce the likelihood of fires occurring before serotinous species such as *P. pungens* (Table Mountain pine) and *P. rigida* are outcompeted by shade-tolerant broadleaved trees, thus selecting against serotinous phenotypes (Zobel 1969; Givnish 1981; Williams & Johnson 1990, 1992). On these sites, in the absence of fire, limited seedling recruitment may occur on sites with low canopy coverage and shallow litter (Fig. 12.13). Likewise, as site productivity decreases, for example on sparsely vegetated rock outcrops, fire frequency declines and *P. rigida* forms uneven-aged non-serotinous populations that persist indefinitely with little threat of being displaced (Abrams & Orwig 1995); the same has been observed for *P. pungens* (Barden 1977a, b). Laessle (1965) has suggested that landscape patterns control serotiny polymorphism in *P. clausa*. In the peninsula of Florida this species forms large contiguous stands that are subject to periodic stand-replacing crown fires, leading to even-aged serotinous populations. In the Florida panhandle, on the other hand, it occurs in small, uneven-aged populations, in a mosaic of more mesic vegetation types and has a fire regime of low-intensity ground fires that generate uneven-aged, non-serotinous populations.

The importance of active selection maintaining serotiny is also suggested by the persistence of serotinous *P. contorta* subsp. *bolanderi* (Bolander pine) on the sandy



Fig. 12.14. ***Pinus coulteri*, a chaparral-oak woodland pine that does not self-prune (photo: J.E. Keeley).**

pygmy forests of northern California, within dispersal distance of non-serotinous populations of *P. contorta* subsp. *contorta* (Critchfield 1957; Westman 1975). Another example would be the Californian *P. coulteri* which has non-serotinous cones in most woodland/forest populations, but an increasing percentage of serotinous cones on trees juxtaposed with chaparral brushlands (Borchert 1985). Chaparral populations of this pine have an even-aged structure resulting from synchronized seed dispersal following stand-replacing crown fires (Vale 1979; Borchert 1985). Woodland/forest populations, however, have an uneven-aged population structure, due to continuous seed dispersal and a fire regime of stand-thinning ground fires (Borchert 1985). Coincident with this pattern is a polymorphic branching habitat (Zobel 1953); on chaparral landscapes it branches near the ground (Fig. 12.14), making canopy ignition almost certain, whereas on forested sites it self-prunes for a considerable length of the bole, increasing the chances of surviving low-intensity ground fires.

Pinus banksiana is a serotinous species closely related to *P. contorta* subsp. *latifolia* that occupies relatively unproductive sites in the boreal forest of North America, being a relatively recent colonizer of glacial sands (Payette 1993; Despons & Payette 1993; Béland & Bergeron 1993). Due to the very short growing season, fuel accumulation is slow and the fire-return interval relatively long – about 100 years – and of sufficient intensity to generate stand-replacing crown fires. High fire intensity appears necessary to release seeds and to destroy competing vegetation, thus both seedling density and growth are positively correlated with fire intensity (Weber, Hummel & van Wagner 1987). Over much of its range it forms even-aged stands with recruitment restricted to the first decade after fire (Cayford & McRae 1983; St-Pierre & Gagnon 1992; Gauthier, Bergeron & Simon 1993a). Despite natural thinning of smaller trees in the first few decades, decomposition is

slow and stands are generally very dense with much standing dead wood (Yarranton & Yarranton 1975; Govindaraju 1984; Stocks 1987; Kenkel 1988), making the site increasingly susceptible to fire. This pattern, however, is affected by site productivity: on less productive xeric sites, populations tend to be uneven-aged as recruitment occurs in gaps (Abrams 1984; Gauthier, Gagnon & Bergeron 1993b) from cones opened by heat generated during the summer on these more exposed sites (Sterrett 1920; Fowells 1965). *Pinus banksiana* is a relatively short-lived species (100–200 years) and if sites escape fires for more than 200 years this species will be displaced by less fire-dependent species such as *Picea mariana* (Gauthier *et al.* 1993b).

Five serotinous pine species are distributed on relatively unproductive sandy or rocky sites in the eastern USA, including several that are vigorous resprouters such as *P. clausa*, *P. rigida* and *P. serotina*, as well as *P. pungens* and *P. virginiana* (Virginia pine). None of these are very long lived but experience fires, typically at 10–50 year intervals, which result in stand-replacing crown fires (Crutchfield & Trew 1961; Zobel 1969; Forman & Boerner 1981). Less intense ground fires are not as effective at inducing pine recruitment for most of these serotinous species (Barden & Woods 1976; Groeschl, Johnson & Smith 1992). Rapid regeneration by resprouting broadleaved species (Webber 1935; Boerner 1981; Buchholz 1983) puts a premium on rapid seedling recruitment from serotinous cones. The southern Mexican and Central American highlands, with a summer-rain climate, also have numerous serotinous species, including *P. greggii*, *P. jaliscana*, *P. leiophylla*, *P. oocarpa*, *P. patula*, and *P. pringlei*.

Serotinous pines are also frequent in summer-droughted mediterranean-climate regions; *P. brutia* (Eastern Mediterranean pine) and *P. halepensis* (Aleppo pine) of the Mediterranean Basin, and *P. attenuata*, *P. contorta* subsp. *bolanderi*, *P. muricata*, and *P. radiata* of Oregon, California and Baja California. These are moderately productive environments with rapid fuel accumulation and annual summer droughts conducive to fires.

Ignition sources are not nearly as ubiquitous as they are in regions such as the southeastern USA; thus fire-return intervals are 10 to 100 years or more (Keeley 1982; Abbas, Barbéro & Loisel 1984; Trabaud, Christensen & Gill 1993). This fire-return interval, coupled with the juxtaposition of these forests with highly flammable shrublands and the lack of self-pruning in most of these pines, nearly always results in stand-replacing crown fires (Vogl *et al.* 1977; Trabaud, Michels & Grosman 1985; Thanos *et al.* 1989; Moravec 1990; Ne'eman, Lahav & Izhaki 1992a). These post-fire environments are different from serotinous pine habitats in other regions in the abundance and diversity of broadleaved seeding species; many of these are annuals capable of rapid growth and vigorous competition. Bond

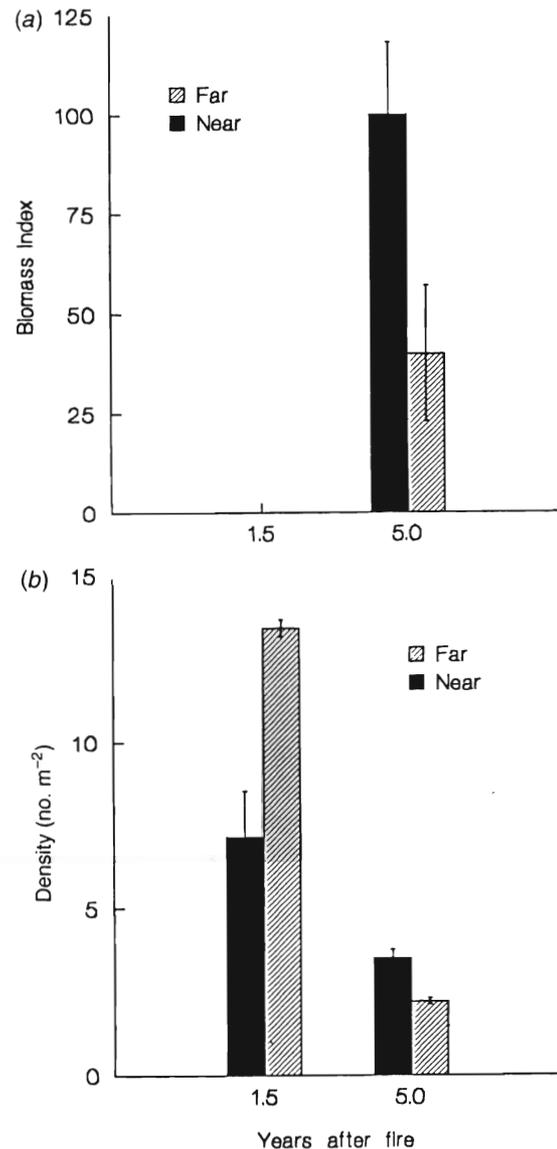


Fig. 12.15. Postfire *Pinus halepensis* seedling density (a) and relative biomass (b) near and far from burned tree skeletons (from Ne'eman 1996).

(1989) hypothesized that such competition should be particularly severe for obligate-seeding species (e.g. serotinous pines) and recruitment would be most successful on sites with reduced establishment of other species. There is evidence that this may be the case for *P. halepensis*, where post-fire competition is markedly reduced near the pre-fire pine skeleton and in this microhabitat pine seedlings are most likely to succeed (Fig. 12.15) (Ne'eman *et al.* 1992a, b; Ne'eman 1997). It is not known how much of this pattern can be explained by the more intense heat likely to be generated within the canopy shadow or by the inhibitory effect of ash on germination (Ne'eman, Meir & Ne'eman 1993a, b). A similar pattern is seen in the Californian serotinous pine forests; a post-fire inhibition of herbaceous growth within the canopy shadow of *P. attenuata*



Fig. 12.16. Postfire herb growth in chaparral (left) compared with relatively depauperate regrowth beneath burned knobcone pines (right) (photo: J.E. Keeley).

skeletons (Fig. 12.16), where pine seedling recruitment is concentrated (G. Ne'eman, J.E. Keeley & C.J. Fotheringham, unpublished data).

Pinus attenuata may also avoid intense post-fire competition by its tendency for establishing on nutrient-poor serpentine soils, a common characteristic of most of the closed-cone conifers in California (Vogl 1973; Vogl *et al.* 1977; Zedler, Gautier & Jacks 1984).

In summary, environments with predictable, high-intensity stand-replacing fires select for resprouting and serotinous adaptations in pines. Most of these pines are relatively short-lived (100–200 years) and become reproductive at an early age (<10 years), and most occur in dense even-aged stands. Nearly all species are polymorphic for serotiny and this appears to be under simple genetic control that can be altered by changes in the fire regime over one to several generations.

12.2.3 High site productivity

One obvious conclusion from Fig. 12.1 is that fire-return interval is not a simple function of site productivity. Pines are most susceptible to displacement by other species on productive sites, and therefore they are, or were before human intervention, dependent on fire disturbance to create opportunities for establishment and early survival. In an oxygen-rich atmosphere, plant biomass is always susceptible to fire when drought or drying conditions coincide with ignition. At one extreme, on some productive sites recurrent drought and frequent lightning ignition can cause high fire frequency which reduces fuel loads and favours understorey species that will be readily burned in less than the most extreme drying conditions. These factors reduce intensity and favour stand-thinning fires rather than stand-replacing fires. In moister situations with less frequent or less extreme episodes of drought, fuel accumulation will be greater, stands denser, and the



Fig. 12.17. Thick bark and self-pruning typical of *Pinus ponderosa* in California's Sierra Nevada (photo: J.E. Keeley).

conditions necessary to propagate fires more extreme, with the result that fires will be rare, but stand-replacing when they do occur. Which position along this continuum of fire conditions a pine species has occupied will determine the evolutionary options that have been open to it.

Productive sites with high fire frequency [predictable stand-thinning fires]

Pinus ponderosa persists in environments with high fire-return intervals such as the mixed coniferous belt of the western USA. Wet winter and spring growing seasons provide sufficient deep moisture to allow large trees to grow and shade out much of the understorey, but woody debris and other fuels accumulate rapidly in the understorey. Summer convection storms ignite dry fuels and have historically led to frequent fires, at intervals of 2 to 20 years, except during the recent fire suppression era (Show & Kotok 1924; Cooper 1960; Lunan & Habeck 1973; McBride & Laven 1976; Kilgore & Taylor 1979; Dieterich & Swetnam 1984; Habeck 1990; Arno, Scott & Hartwell 1995). Limited understorey reduces the chances that fire will enter the canopy and destroy adult trees, and these conditions have selected for attributes that enhance survival of frequent moderate-intensity fires: self-pruning of dead branches and thick bark (Fig. 12.17). Fires in these forests burn in a mosaic pattern of low-intensity ground fire interspersed with flare-ups that are lethal to (1) patches of more shade-tolerant species, (2) younger denser stands of trees with sufficient 'ladder fuels' to carry fire into the canopy, or (3) susceptible diseased or damaged trees (Agee, Wakimoto & Biswell 1978; Harrington 1987a; Kalabokidis & Wakimoto 1992; Chap. 11, this volume). Post-fire recruitment is largely restricted to these highly localized sites of crown fire, from seed sources in adjacent sites subjected to lighter ground fire.

A mosaic burning pattern with highly variable local intensity at a small scale makes invisable patches available

to the fire-resistant mature trees whose cone crops are high in the tree and can survive even severe crown damage (Rietveld 1976). *Pinus ponderosa* seeds are winged and disperse within a 100 m radius, allowing them to saturate small patches suitable for seedling establishment. This recruitment pattern leads to even-aged patches of *P. ponderosa* on the scale of <0.5 ha (Cooper 1960; West 1969; Agee 1993). Within these patches certain trees will dominate, resulting in a very uneven-sized distribution (Knowles & Grant 1983), and the suppressed trees are likely to be thinned out in a subsequent fire. On some sites successful recruitment may be uncommon (White 1985); however, due to their longevity (>700 years; Swetnam & Brown 1992), forest equilibrium will persist if successful establishment occurs roughly every 500 years for each individual in the community. Serotiny is clearly not essential or necessarily even advantageous for a species which can survive multiple fires and is presented with many opportunities for establishment during its lifetime.

Though *P. ponderosa* thrives with frequent fire, under many circumstances it can survive without it. For example, on arid margins of its range, *P. ponderosa* recruitment occurs in gaps created by natural mortality or in brushfields or grasslands (Mirov 1967; Vale 1977; McTague & Stansfield 1994). On these arid margins fires are less frequent or rare and recruitment is more continuous and less restricted to temporarily available patches (West 1969). On some nutrient-deficient arid sites, *P. ponderosa* may have a marked competitive advantage over broadleaved shrubs and herbs (DeLucia, Schlesinger & Billings 1989). As site aridity increases seedlings of this species cannot maintain adequate water balance (Barton 1993). On the high-elevation edge of its distribution, *P. ponderosa* stands lack recruitment, possibly due to historical climate change (Stein 1988), or replacement by the more cold-hardy *P. jeffreyi* (Haller 1959) and both are replaced on moister sites by *P. lambertiana* (sugar pine) (Yeaton 1981). All three of these montane pines have a nearly identical mode of resisting fire through thick bark, self-pruning, and crown heights of 40–60 m. If the fire regime is altered by fire suppression, fuel accumulation results in local extirpation (Kilgore 1973; Talley & Griffin 1980; White & Vankat 1993; Habeck 1994).

Some highly productive sites in the mid-western and eastern parts of Canada and adjacent USA also experience high-frequency, low-intensity stand-thinning fires. Using charcoal stratigraphic analysis and fire scars on *P. resinosa* (red pine), Clark (1990) estimated the mixed conifer/hardwood forests of Minnesota had experienced fires at 8–13 year intervals over the last 750 years, and similar fire-return intervals have been reported from red pine fire scars in northern Vermont (Engstrom & Mann 1991). Mature *P. resinosa* survive these fires due to the unusually

fire-resistant thick bark (van Wagner 1970) and extensive self-pruning that eliminates ladder fuels that would lead to stand-replacing crown fires; Fowells (1965) noted that this pine self-prunes better than any other conifer. Seedling recruitment for *P. resinosa* shares an important feature with the western *P. ponderosa*; low-intensity ground fires that burn surface fuels are insufficient for recruitment; rather, seedling, establishment requires local flare-ups that remove patches of vegetation, creating an even-aged patchwork mosaic (Butson, Knowles & Farmer 1987; Roberts & Mallik 1987; Bergeron & Brisson 1990; Engstrom & Mann 1991; Flannigan 1993).

Highly productive sites with unpredictable fires [unpredictable stand-replacing fires]

Highly productive sites in climates lacking an annual summer drought produce vegetation with high fuel moisture and therefore a low probability of fires propagating. This does not preclude fires, but it means that they are rare and unpredictable, and when they do occur are high-intensity and stand-replacing fires (Whitney 1986; Clark 1993). Other disturbances, both large- and small-scale, such as windthrow, insect outbreaks, and extreme drought therefore play a more prominent role in community dynamics. These circumstances require species that have some tolerance of closed-canopy conditions while also favouring species that can exploit the rare opportunities for invasion of disturbances. Highly specialized traits favouring fire survival or immediate post-fire seedling establishment at the cost of establishment at other times will tend to be selected against. Pines of subsection *Strobi* are the group that seems best equipped to deal with these constraints and opportunities. For example, *P. strobus* (eastern white pine) of the eastern and midwestern USA does not necessarily require large disturbances, burned sites or mineral soil to survive. It can exploit small gaps and small disturbances (Abrams, Orwig & Demeo 1995; Ziegler 1995). But it also is a vigorous invader of sites disturbed by wildfires or, more commonly, by hurricanes through wind dispersal of light winged seeds from surviving trees. Colonization can occur either in the first years after fire, or into early-successional forests 15–20 years after the fire (Goff 1967). Rapid growth and tall stature are essential for these species to gain a foothold before the sites are closed to invasion by more shade-tolerant broadleaved trees (Goff & Zedler 1968; Ahlgren 1976; Leak, Cullen & Frieswyk 1995).

Pinus strobus is one of the tallest pines, often towering over the surrounding hardwood forest. Because of its moderately long lifespan, it may persist long after other pines have perished (Fig. 12.18). Height is also of selective value because it increases the chances of seed falling on new disturbed sites.

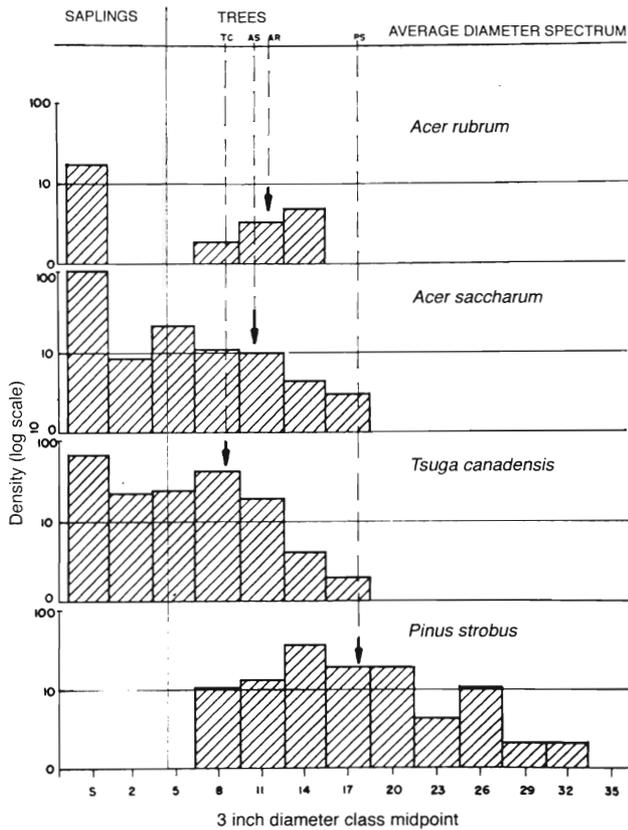


Fig. 12.18. Size distribution of dominant trees in upland forests in the Great Lakes area of the Midwestern USA (from Goff & Zedler 1968).

This life history has provided little selective pressure for fire-resistant morphology or growth patterns. Thick bark and self-pruning of lower branches are of minimal value (Landers 1991), because a given site may not burn for a thousand years; however, local extinction is a possibility (Whitney 1986). But within a landscape with suitable soils, extinction of *P. strobus* at larger scales is extremely unlikely. Over long periods of time, the regional population of *P. strobus* probably shifts considerably in its pattern and overall abundance, replacing or being replaced by other pines such as *P. resinosa* primarily in response to changes in fire pattern and temporal regime (Fig. 12.19).

Other species in subsection *Strobi* have life-history characteristics that are broadly comparable to the well-studied *P. strobus*. In the western USA, *P. monticola* (western white pine), like the eastern white pine, is a long-lived forest species of intermediate tolerance and limited fire resistance that occurs primarily on mesic, and therefore in the west, higher-elevation habitats (Fowells 1965; Cwynar 1987). It readily invades burned sites (Agee & Smith 1984; Morrison & Swanson 1990), but on mesic sites, in the long absence of fire, it is displaced by more shade-tolerant conifers (Huberman 1935; Parker 1988). On extreme sites it can play a role in primary succession (Jackson & Faller 1973) where it may intergrade with timberline species dis-

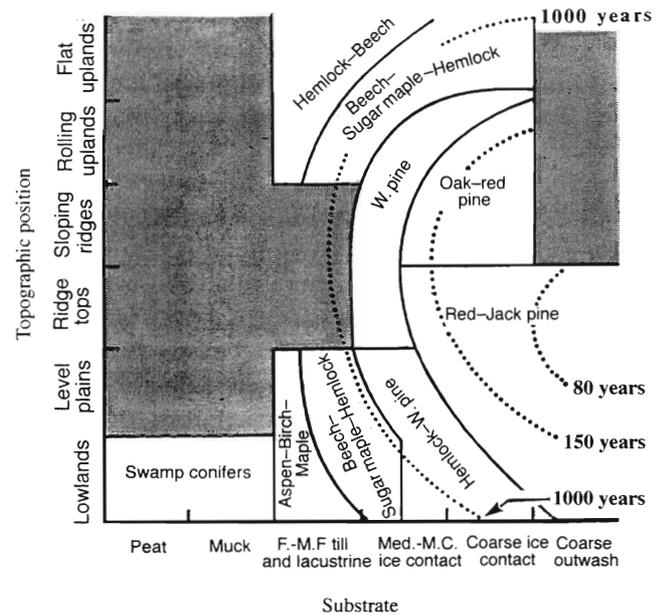


Fig. 12.19. Distribution of jack pine (*Pinus banksiana*), red pine (*P. resinosa*), and white pine (*P. strobus*) along topographic and substrate gradients in Michigan (from Whitney 1986).

cussed above. In light of this broad ecological amplitude it is consistent that Rehfeldt (1984) described this species as having a generalist genotype.

Another Californian species in the white pine group, *P. lambertiana*, is a characteristic component of montane forest over a considerable latitudinal range, but is rarely dominant. Where it occurs, it is often among the largest trees; it can also achieve great age (Fowells 1965). Its large size confers some degree of fire resistance on the oldest individuals, and its distribution therefore overlaps those of the more fire-demanding and fire-tolerant *P. jeffreyi* and *P. ponderosa*. Like white pine, *P. lambertiana* can invade recent burns (Talley & Griffin 1980), but its shade tolerance also permits saplings to persist beneath the canopy of other trees or in small openings, providing it with an ability to exploit small gaps. Its seedlings germinate in either mineral soil or litter (Rundel *et al.* 1977).

Mexican members of subsection *Strobi*, e.g. *P. ayacahuite* (including var. *strobiformis*) and *P. chiapensis*, occur in montane habitats where rainfall is higher and more reliable, generally as subdominants or in small groves (Perry 1991). These are sites where productivity is higher, competition from other conifers and broadleaved trees is more a factor, and fires, at least until recent centuries, are rare.

In the southeastern USA, a group of pines in subsection *Australes* lacks obvious adaptations to fire beyond a marked ability to invade disturbed areas, including burns. These species have high growth rates, relatively short lifespans, and produce an abundance of readily dispersed seeds, and

some have specific adaptations to tolerate flooding (Knight *et al.* 1994). For species of moist lowland sites, such as *P. glabra* (spruce pine) and *P. taeda* (loblolly pine), natural fires were rare and unpredictable within their relatively short lifespan (Landers 1991). But despite this, both species colonize burns that occur on better-drained soils. When established on the uplands where fires are more common, the adults tolerate low-intensity ground fires, but the seedlings and saplings are generally killed (Garren 1943; Oosting & Livingston 1964; Landers 1991). *Pinus elliottii* (slash pine) is a widely distributed species with similar life-history characteristics which can occur on moist sites. It is also an aggressive colonizer of burned forests. The proportions of these pine species will vary with soil drainage, topographic position, and proximity of seed sources as well as fire regime.

Unlike more obviously fire-adapted species, they cannot withstand repeated burning and their long-term dynamics is dependent on re-invasion (Mattoon 1922; Borman 1953; Cooper 1957; Clewell 1976; Gibson & Good 1987; Landers 1991, Doren, Platt & Whiteaker 1993). Under natural conditions it is likely that on moist sites, fires were not the most important disturbance. The southeast is subject to hurricanes and tornadoes and the invasion of pines into the devastated areas has produced large, even-aged stands of these species so often that the names 'hurricane forests' (Turner 1935) or 'harricans' (Doren *et al.* 1993) have entered into the local language.

Several pines in other parts of the world have a similar ecology and lack of specific adaptation to fire but clear dependence upon a successional role on disturbed sites, e.g. the European *P. nigra* (Trabaud & Campant 1991; Regato-Pajares & Elena-Rosselló 1995) or the Japanese *P. densiflora* (Nakagoshi, Nehira & Takahashi 1987). *Pinus sylvestris* (Scots pine), which because of its vast range and occurrence in highly varied habitats (Walter 1968), must also be considered one of the great successes of the genus. Like other pines, Scots pine has a high-light requirement (Kreeb 1983) and it is therefore never a climax species where a lack of disturbance or suitably favourable conditions permit shade-tolerant species to be strong competitors. Its present wide distribution may, in fact, be considered as the premier example of a pine exploiting disturbance, in this case the vast continent-wide 'disturbance' of glaciation (Pravdin 1969; Chap. 5, this volume). Like many of the species discussed above, it is a generalist colonizer in more heavily forested regions (Steven & Carlisle 1959), and is dependent on fire or, more recently, humans for its persistence as a dominant (Uggla 1974). In marginal situations such as in the far north, fire is not necessary for *P. sylvestris* to persist, and it exists in permanent stands with mixed-age populations sustained by rare waves of regeneration related to climatic variation

(Zackrisson *et al.* 1995). Like widespread species of North America, *P. sylvestris* shows considerable variation over its range (Carlisle 1958; Mirov 1967; Pravdin 1969; Vidaković 1991), suggesting that there has probably been selection in each region which has fine-tuned the physiology, morphology, and life history.

12.3 Role of ecological strategies in determining patterns of cone production, seed germination, and predation

12.3.1 Cone development and pollination

Pines are monoecious, with male strobili typically on tertiary or higher-order branches lower in the crown and female strobili on more vigorous main shoots in the upper part of the crown (Owens 1991). Strobili or cone primordia are initiated in the growing season prior to their appearance and 9–12 months before pollination; thus, in seasonal environments they undergo a winter dormancy prior to opening. There is evidence that haploxyton pines differentiate primordia later and have a shorter developmental period than diploxyton pines (Fowells 1965; Mirov 1967; Owens 1991).

The timing of the release of the wind-dispersed pollen appears to be controlled by local conditions, beginning in January at low latitudes and low elevations and extending into late summer at high latitudes and elevations (Young & Young 1992). Self-fertilization is possible, but generally has been observed to lead to reduced seed set (Chap. 14, this volume). The spatial separation of the two sexes of strobili is therefore probably a means of decreasing self-pollination (Forshell 1974; Smith, Hamrick & Kramer 1988; Sorensen 1994). Once in place, the growth of the pollen tube from the pollen grains is slow, and typically undergoes a winter dormancy period prior to fertilization, usually one year after pollination.

Seeds develop rapidly and mature and disperse about six months later, generally in the second autumn after pollination. In a few species the seed maturation period is longer, e.g. *P. leiophylla*, *P. maximartinezii* and *P. pinea* (Donahue & Lopez 1995). In some species there is a delay in seed dispersal, which varies from a few months to many years in the case of strongly serotinous species. Three Californian pines (*P. coulteri*, *P. muricata* and *P. radiata*) illustrate further complexities of seed release. All are polymorphic for serotiny but the non-serotinous cones delay dispersal until mid- to late winter, despite the fact that seed maturation is completed by early autumn (Sudworth 1908; Burns & Honkala 1990; Young & Young 1992). Thus even these 'open cones' would be functionally serotinous

since dispersal would be after the natural fire season, which is typically during autumn, at the end of the summer drought, when Santa Ana *föhn*-type winds result in the most extensive wildfires. Delaying dispersal could have another selective basis since it may reduce predation by limiting the time seeds are on the ground prior to predictable rainfall.

The 2+ year reproductive cycle in pines (Chap. 13, this volume) may limit life-history evolution, an obvious constraint being the impossibility of an annual growth habit. It is unknown whether this long reproductive cycle is an effectively irreversible trait rooted deeply in ontogeny, or if it is a trait maintained by current selection. Certainly the glacial pace of pine pollen tube growth is amazing in comparison to the seemingly instantaneous rate of angiosperms. As Bond (1989) has observed, *Zea mays* pollen tubes can traverse the centimetres-long styles of the maize tassel and effect fertilization in hours, whereas pine pollen requires nearly a year to complete the same task. A key difference that may point to the selective value of delay is that angiosperms are required to commit resources to ovule development before 'knowing' whether or not pollination was successful, whereas in pines unsuccessful pollination has lower costs, since the megaspore does not initiate megagametophyte development until after pollination is completed (Mirov 1967; Chap. 13, this volume). While this slow pace of pollen tube development appears to be unique to gymnosperms it may be a response to winter dormancy as it apparently is not characteristic of tropical pines (Mirov 1962). Other features of the long reproductive cycle are not unique to gymnosperms. Numerous angiosperms initiate floral primordia 9–12 months in advance of pollination and there are *Quercus* species throughout the Old and New Worlds that require up to 18 months following pollination for seed maturation.

Cone size varies by an order of magnitude within the genus, from 2 to 50 cm. This variation is only partly related to seed size (Fig. 12.20). For example, an analysis of log-transformed cone length and seed length data for the Mexican pines from Perry (1991) shows no overall relationship between cone size and seed size ($r^2=0.004$, $p > 0.60$, d.f.=67). But when the species are grouped as 'arid' and 'mesic', a significant trend is found within the more numerous smaller-seeded mesic group ($r^2=0.46$, $p < 0.0001$, d.f.=53) but little improvement within the larger-seeded arid group ($r^2=0.01$, $p > 0.69$, d.f.=13). The other pattern that emerges is that arid (mostly pinyon-type) species have on average smaller cones (6.4 vs 11.7 cm). The large seed size of arid pines is explained by the combination of an animal dispersal syndrome with the need for seedlings in arid regions to get a strong start in the first season. It is less clear why cones should be smaller;

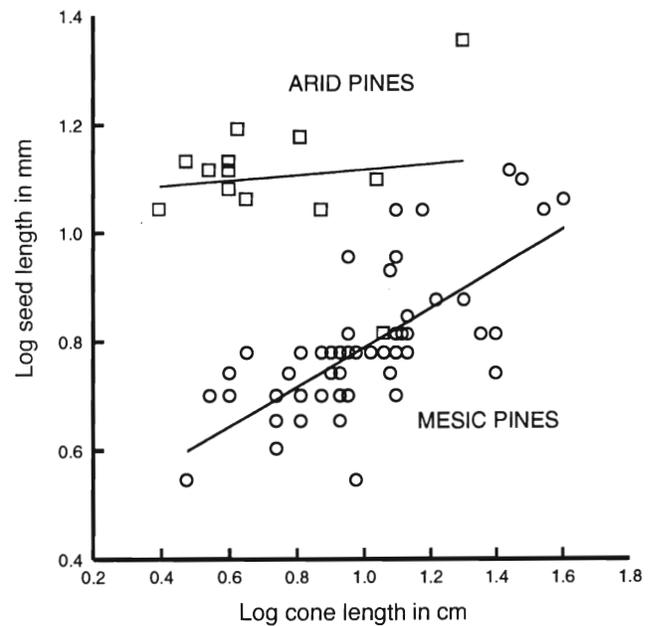


Fig. 12.20. Relationship between seed-wing length and cone length for arid-adapted and mesic-adapted Mexican pines (data from Perry 1991).

however, these pines have a relatively high ratio of seeds to cone biomass, something of potential selective value in these unproductive environments.

In addition to the larger between-species variation, there is often large intraspecific variation. One example is *P. sabiniana* from the interior of California which produces very small cones in the northern portion of its range and cones more than twice as large in the southern part of its range (Stockwell 1939).

12.3.2 Patterns of cone production

Pine species vary by more than an order of magnitude in their age of first reproduction, ranging roughly from 5 to 50 years (Strauss & Ledig 1985). As a general rule, species in high fire frequency habitats begin reproduction earlier than others. Timberline and desertic species tend to delay initiation of reproduction, but some species in moderately productive environments (e.g. *P. lambertiana*) also delay reproduction for many decades.

Periodicity and magnitude of cone crops varies greatly between pine species. Many are noted for mast years at intervals of 3–10 years, whereas others produce similar-sized crops each year (Fowells 1965). Mast fruiting of course is of little value for serotinous species and as will be shown in the concluding section is not characteristic of such pines. In other species there is evidence that mast fruiting may play a role in predator satiation. Annual *P. ponderosa* cone production over a 10 year period ranged from about 800 to > 11 000 per hectare and percentage cone predation by squirrels was inversely related to crop

size (Larson & Schubert 1970). However, there is evidence that excessive commitment of resources to large cone crops may carry with it a cost; high cone production in *P. edulis* was significantly related to degree of insect herbivory the following year (Forcella 1980).

In light of the length of time from strobili initiation to seed dispersal, it is not surprising that factors affecting size of cone crops are not well understood, particularly in species with high variance in annual production. Abiotic factors, especially weather, external biotic factors such as predation, or even internal competition for photosynthate and other nutrient pools between the previous and current year's cones, could all potentially affect the size of cone crops at the stage of strobilus initiation, pollination, and seed maturation. Thus, broad generalizations about factors controlling cone production are lacking, but some patterns are evident. For example, two independent studies reported that high temperatures during strobilus initiation were significantly correlated with cone crop size 2+ years later in *P. ponderosa* (Maguire 1956; Daubenmire 1960) and the same has been observed for *P. resinosa* (Lester 1967). Reduced water stress around the time of strobilus initiation has likewise been correlated with high cone crops in *P. elliotii* (Varnell 1976), *P. monticola* (Rehfeldt, Stage & Bingham 1971) and *P. taeda* (Dewers & Moehring 1970). For *P. monticola*, early-summer water stress in the year following pollination was correlated with strobilus abortion. Although such a conclusion may be premature, it appears that environmental factors early in the reproductive cycle are more critical than later in the cycle.

12.3.3 Seed germination

Given adequate moisture and temperatures, seeds of most pines will germinate readily following release from the cone. In fact, pine seeds germinate so readily that sometimes this happens before they are dispersed. In a form of *P. heldreichii* var. *leucodermis* some seeds germinate and start seedling development while still in the cones (Tucovic & Stilnovic 1972). Some species, especially those of high latitudes or high elevations, require a cold (<5 °C) stratification treatment, or such treatment speeds the rate of germination (Young & Young 1992). However, generalizations are dangerous as seeds of some high-elevation species, e.g. *P. aristata*, will germinate without pre-chilling. Nor is germination behaviour uniform within species. Some differences have been attributed to ecotypic response to incubation temperature (Haasis & Thrupp 1931), and many environmental factors have been shown to affect germination including pretreatment scarification of the seed coat, light, and temperature during germination. In some pines there is an interaction between light and stratification; light eliminated the dependence on cold stratification for *P. ponderosa* (Li, Burton & Leadem 1994), whereas in the

European *P. heldreichii* no such interaction was observed (Borghetti *et al.* 1989). Such complexity is commonplace in seeds of many species and illustrates the need for field studies combined with factorial laboratory experiments.

In most pine habitats, conditions suitable for pine seed germination are met within months of dispersal, thus it is not surprising that there is little or no annual seed carry-over in the soil (Quick 1956; Pratt, Black & Zamora 1984). Seeds of some pines have been shown to germinate poorly under closed canopies or heavy litter (Harrington & Kelsey 1979) and allelopathy may play a role (Harrington 1987b). But seeds on the ground that do not germinate in the first growing season are not likely to survive long due to predation and those that do will lose viability within a year or two (Wahlenberg 1960; Fowells 1965; Johnson & Fryer 1989).

Seed viability can be maintained over many years when seeds are retained within serotinous cones. Germination will be little impaired for five years in closed cones and, although viability does decline with age, some viable seeds may remain after a decade or more (Badron 1949; Andresen 1963; Barden 1979; McMaster & Zedler 1981; Borchert 1985). Seeds that are dispersed after fire may be affected by the pattern of fire intensity within the site. Germination is inhibited by ash in *P. halepensis* (Ne'eman 1993a, b) and *P. banksiana* seeds (Thomas & Wein 1994) and for the former species this appears to have important implications for the spatial distribution of seedlings (Fig. 12.15).

12.3.4 Life history evolution and coevolution

Herbivory and parasitism

Animals have assuredly had a long evolutionary association with pines, both as predators and dispersers. But despite a respectable collection of studies that have explored evidence of coevolution in both vegetative and reproductive traits, no attempts have been made to explain animal-plant interactions for the genus as a whole.

Pine resin, though probably performing many functions, is certainly a key element in plant-animal interactions. Pine resins contain toxic terpenes and there is much species-specific variation in their monoterpene composition. Associated with this are species-specific parasites and predators that have evolved tolerance to these compounds. The level of specificity in the interaction is illustrated by the clonal scale insect (*Nuculaspis californica*) which occurs on *P. ponderosa*. It has differentiated into separate demes on individual trees in response to differences in xylem and phloem monoterpenes (Edmunds & Alstad 1978).

For mammalian predators that can move among trees, the response to individual pine variation is behavioural

(Pederson & Welch 1985; Zhang & States 1991). Thus, tassel-eared squirrels can select *P. ponderosa* trees with smaller amounts of monoterpenes than in trees of the same species not used as food sources (Thomas 1979; Farentinos *et al.* 1981), and selected trees suffer significant reductions in several fitness components (Snyder 1992, 1993). Individual differences in susceptibility to insect predation on seeds have also been noted for this pine species (Schmid, Mata & Mitchell 1986). Evolving resistance to such parasitism/predation is possibly complicated by the fact that resistance to one predator, such as the bark beetle (*Dendroctonus*), apparently does not involve the same phloem chemistry as resistance to a parasite such as dwarf mistletoe (*Arceuthobium*) (Linhart, Snyder & Gibson 1994).

It is curious that conifers appear to be more susceptible to tree-killing insect predators than angiosperms; for example, bark beetles (Scolytidae) are responsible for over half of all natural deaths in over-mature conifers and are known to decimate entire forests, particularly if trees have been weakened by drought or other stresses (Ohmart 1989; Chap. 18, this volume). While phylogenetic and energy allocation constraints may explain this pattern, there may be indirect explanations, such as the adaptive value of the consequent increased probability of stand-replacing wildfires in these over-mature forests (Mutch 1970; Bond, Maze & Desmet 1995). Another view would be to attribute this problem to the tradeoffs that are necessary in life-history evolution. Pines generally, and especially those that face competition from other tree species, are adapted to catching disturbance-generated waves and riding them – staying ahead of more shade-tolerant competitors by virtue of rapid growth and an ability to exploit open conditions. It is reasonable that species with this life-history mode might evolve more general defences that are dependent on vigour. Thus bark beetles are fended off in healthy trees by ‘pitching out’, a defence lacking in subtlety and very effective while trees are healthy, but subject to failure when trees are stressed (Speight & Wainhouse 1989). Further, the correlation of pine establishment and disturbance would mean that pine populations would tend to have narrower age distributions than many angiosperms. This too might make them susceptible to outbreak. Finally, as with senescence in animals, there may historically have been a correlation between the onset of susceptibility of pines to insects and a significant decline in the prospect of future offspring. If so, selection for alternative means of resistance may have been weak. Pines can tolerate such episodes of mortality so long as the ecosystem continues to serve up large disturbances at the required frequency.

We can expand the realm of coevolutionary scenarios by considering the hypothesis of Rice & Westoby (1982), which argues that complex life cycles have evolved in heteroecious rusts as a means of making them agents of

interference competition by angiosperms against conifers in a kind of primaevial biological warfare. For example, some rust fungi, such as white pine blister rust, are potentially lethal to the teliospore host pine but much less damaging when present in the aecial stage on host *Ribes* shrubs (see also Chap. 19, this volume). This asymmetry suggests it is possible that the fitness of infected *Ribes* might be greater than non-infected individuals because they inoculate the overstorey pines, causing mortality which could open the canopy and create opportunities for *Ribes* colonization. It is not clear, however, that the selection coefficients would be consistent enough to promote such a complex balance. Among other questions is whether pines can use such a system to their advantage in eliminating hardwoods.

Certain life-history characters may have unexpected impacts on other aspects of the life history. For example, Smith & Balda (1979) noted that five orders of insects, six families of birds, and two orders of mammals in various combinations can exploit the cones and seeds of most pine species. However, *P. contorta* is an exception to this pattern because only one squirrel and one coreid bug attack its serotinous cones. They hypothesized that the ever-present cone crop in this species, coupled with the low annual variance in cone crop size, allowed for competitive exclusion of most predators. In other pines, very high variance in magnitude of annual cone crops prevented exclusion by maintaining predator populations in perpetual disequilibrium.

Herbivory can significantly alter reproductive patterns. *Pinus edulis* trees attacked by the moth *Dioryctria albobittella* over a period of years produced over 40% less wood and, due to the pattern of herbivory, buds that would differentiate into female strobili were destroyed, producing functionally male plants (Whitham & Mopper 1985).

Granivory and seed dispersal

Smith (1970) hypothesized that discriminatory feeding behaviour of squirrels (*Tamiasciurus* spp.) could act as selective agents and alter pine life-history characteristics. He compared the serotinous *P. contorta* var. *latifolia* with the open-cone *P. contorta* var. *murrayana*. Serotinous cones serve as a year-round food source and Smith assumed that for serotinous species there must be intense selection for cones that are harder, more asymmetrical, and shorter-stalked than cones from the non-serotinous variety. Increased allocation of resources to cone protection may explain why var. *latifolia* has fewer seeds per cone; but it is also possible that squirrels select against high seed numbers because they choose cones with more seeds in an effort to maximize their feeding rate (Elliott 1974).

These arguments of animal-driven selection are convincing, but determining the degree to which cone

characteristics are predator-driven is complicated by the role of fire. High-intensity fires could select for harder, asymmetric, sessile cones which would reduce the chances of ignition and thus better protect seeds. Since the open-cone variety *murrayana* is a subalpine tree not subjected to the same fire regime (see above), it is not possible to distinguish between the importance of fire and seed predation. Linhart (1978) encountered the same problem in distinguishing between the selective influence of fire and squirrels on cone morphology in Californian closed-cone pines. Axelrod (1980) contends that interactions with present-day faunas cannot explain traits that originated more than 10 million years ago, although he does not rule out a role for ancestral seed predators. He also is sceptical that fire has been a major factor in cone evolution, a remarkable assertion that runs counter to our view that pines and fire have probably been inextricably linked since the genus originated.

Sorting out the role of extinct faunas is highly problematic, but for a genus of such great antiquity and apparent uniformity over time, it may be necessary if we are to have a clear understanding of the evolution of some pine characteristics. For example, the massive cones of *P. coulteri*, which are the heaviest (up to 2.3 kg) and hardest of all pines and with massive hooked, spine-like apophyses (>5 cm), seem spectacularly over-designed for protection from any extant animal (it has been humorously suggested that they were designed to maim anyone attempting to cut down the tree). It is possible that some elements of the megafauna that disappeared at the end of the Pleistocene (Diamond 1992) may have preyed on these cones. The predation, to be selectively important, would have to be on cones still on the tree. This suggests an arboreal animal or, as Coulter pines are often relatively small trees, perhaps a very large animal that could push over or uproot trees in the manner of elephants.

The Pleistocene extinctions may make it difficult to understand other pine life-history traits. These massive mammals would have generated disturbances of a type and on a scale that cannot be equalled by the historic fauna, and which may have provided opportunities for pine establishment. Quite possibly some pines, that today only recruit after fire, may have evolved under a very different disturbance regime. This is suggested by contemporary studies in Africa, which show that anthropogenic-driven extinction of modern elephants, the major disturbance-creating megaherbivores, leads to the expansion of shrublands and woodlands and a switch from low-intensity stand-thinning fires to more catastrophic stand-replacing wildfires (Owen-Smith 1988).

Cone and seed predation is not restricted to serotinous pines. For example, Tevis (1953) described the near complete decimation of one year's *P. lambertiana* seed crop;

prior to cone opening squirrels cut cones from the tree and woodpeckers slashed them, and seeds were extracted by jays and numerous perching birds. Seeds that reach the ground are probably even more at risk, and are subject to intense predation from mice, chipmunks and squirrels (Martell 1979; Vander Wall 1994). For *P. jeffreyi* and *P. ponderosa* seeds, Vander Wall (1994) estimated a half-life on the ground of 120 hours and predicted that <<1% of the seed crop would go undetected by seed predators. It has been suggested that this predation may favour crypsis and different colour morphs to match substrates (Ager & Stettler 1983) and may account for why the seed wing is readily detachable in most species.

Not all seed removal, however, represents predation because seeds are often not recovered from caches. In fact, Vander Wall (1992) estimated that in one year over 40% of successful seedling recruitment in *P. jeffreyi* came from seed caches, and the mean distance of animal dispersed seeds 13 to 25 m. Further, based on simulated seed fall, he proposed that animals were quantitatively more effective in the dispersal of winged pine seeds than wind. However, maximum dispersal distances are potentially greater by wind than by ground-dwelling rodents, and therefore a combination of wind and animal dispersal may be optimal. The importance of rodent seed predators to the dispersal and planting of seeds is likely to be widespread in pines and has been documented for others such as *P. strobus* in the eastern USA (Abbott & Quink 1970) and the Asian *P. koraiensis* (Hayashida 1989).

The North American timberline *P. albicaulis* and Euro-Asian timberline stone pines (subsection *Cembrae*) share cone and seed characteristics that reflect a long evolutionary symbiosis, with birds in the genus *Nucifraga* (nutcrackers) playing a near-obligate role as dispersal agents (Paryski 1971; Tomback 1981; Lanner 1982, 1990; Chap. 14, this volume). This coevolved mutualism leads to a greatly enhanced chance of seeds reaching safe sites within the subalpine environment and is mandatory for colonizing occasional burn sites. In addition, it makes it possible for these pines to occasionally colonize sites tens of kilometres distant (Tomback 1982; Tomback *et al.* 1990).

There seems little doubt that this is a coevolved system, because of the otherwise inexplicable cone and seed characteristics. These pines – both New World and Old World species in the subsection *Cembrae* – have truly indehiscent cones; unlike serotinous cones that open with heat, these cones, even after falling from the tree, require mechanical opening by snapping off the cone scales along a unique fracture zone that exposes the seed. In addition, these cones lack the armature characteristic of many others, particularly serotinous pines. The timberline *P. flexilis*, in a different subsection to *P. albicaulis*, illustrates remarkable convergence in its large wingless seeds

dispersed by Clark's nutcrackers (Woodmansee 1977; Lanner, Hutchins & Lanner 1980). *Pinus aristata*, on the other hand has smaller winged seeds, yet it too is dispersed to some extent by nutcrackers (Lanner, Hutchins & Lanner 1984).

Desertic pinyon pines are similar to timberline pines in their large wingless seeds that are dispersed by pinyon jays (*Gymnorhinus cyanocephalus*) and nutcrackers (Vander Wall & Balda 1977; Ligon 1978; Styles 1993; see also Chap. 14, this volume) and, as seems to be the case with timberline species, caching behaviour of pinyon jays leads to planting of seeds in seemingly more favourable sites for seedling establishment (Ligon 1978).

12.4 Conclusions on life-history evolution in pines

We view life-history evolution in pines to be driven by the interaction of site productivity and fire frequency, and these factors are correlated with particular structural and functional syndromes. To explore the extent to which fire regimes outlined in Fig. 12.1 can drive pine life-history evolution we have done a principal components analysis similar to the one presented by McCune (1988). Our analysis differs in the inclusion of European and Asian species and a slightly different set of variables. Data came from Fowells (1965), Strauss & Ledig (1985), Loehle (1988), McCune (1988), Landers (1991), and papers referred to earlier in the text. The decision as to which species to include was based on availability of data for all variables, although some species were not included because we lacked a clear understanding of their natural fire regime. For example, *P. contorta* var. *murrayana* possibly does not regularly experience any one of the fire regimes outlined in Fig. 12.1; depending on elevation it may experience no fires, or ground fires or even crown fires. Other pines difficult to assign to a particular fire regime include *P. coulteri* (evidence presented above suggests that it may persist under various fire regimes) and *P. torreyana* (its restriction to coastal bluffs and its relatively short lifespan suggest it may have evolved under an unpredictable fire regime, but this is debatable).

For the 38 species (see Appendix 12.1) used in the principal components analysis (Fig. 12.21), fire regime explained 29% of the variance in the 13 life-history characters (Table 12.2). Life-history characteristics clearly separate species in some fire-regime environments and the component loadings (Table 12.3) indicate that a different set of characters separates species on axis 1 and 2. Here we will discuss the life-history attributes that are correlated with these five fire regimes.

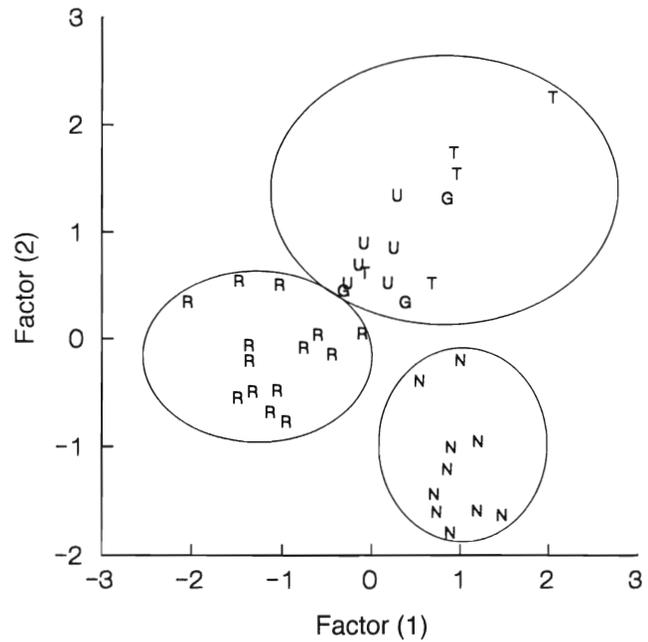


Fig. 12.21. Principal components analysis for 38 pines from the five fire regimes illustrated in Fig. 12.1. N, no predictable fires; G, predictable ground fires; R, stand-replacing fires; T, stand-thinning fires; U, unpredictable stand-replacing fires. Based on 13 characters listed in Appendix 12.1; data from Sudworth (1908); Fowells (1965); Peterson (1967); Strauss & Ledig (1985); Elias (1987); McCune (1988); Loehle (1988); and Perry (1991).

12.4.1 Environments with no predictable fires

These are timberline and desertic pines adapted to extreme site conditions, which are largely fire-free unproductive sites. Pines from these habitats separated clearly along both axis 1 and 2 (Fig. 12.21). Extreme temperatures and short growing season are likely to have selected for their slow growth rates and short stature. Low growth rates may have selected for the long juvenile period and extremely long intervals between mast reproductive years (Table 12.2), and these, coupled with poor recruitment success, may have selected for the great longevity observed in these pines. The lack of predictable fire in these environments has resulted in little self-pruning (indeed, extreme temperatures may select against it) and thin bark (Table 12.3). The fact that these pines are found on abiotically stressful sites is a powerful argument against extreme temperatures and aridity playing a role in the evolution of bark thickness in pines and for fire as an important selective agent.

The dominant factor separating these pines from fire-adapted species is in the measure of dispersability, specifically the ratio of seed-wing length/seed weight (Table 12.3), reflecting the importance of bird dispersal in timberline and desertic species. These pines have substantially larger seeds (Table 12.2) and a different allometric relationship between seed weight and wing size/shape (Benkman 1995b). Considering the whole

Table 12.2. Life-history characteristics (means \pm SE) for species classified by fire regime (letter designations for fire regimes are same as those plotted in Fig. 12.21)

	No predictable fires (N)	Predictable ground-fires (G)	Predictable stand-replacing fires (R)	Predictable stand-thinning fires (T)	Unpredictable stand-replacing fires (U)
Species	<i>albicaulis</i> <i>aristata</i> <i>balfouriana</i> <i>cembra</i> <i>cembroides</i> <i>edulis</i> <i>flexilis</i> <i>monophylla</i> <i>quadrifolia</i> ^a <i>sibirica</i>	<i>elliottii</i> var. <i>densa</i> <i>merkusii</i> <i>palustris</i>	<i>attenuata</i> <i>banksiana</i> <i>brutia</i> <i>clausa</i> <i>contorta</i> subsp. <i>latifolia</i> <i>echinata</i> <i>halepensis</i> <i>leiophylla</i> <i>muricata</i> <i>pungens</i> <i>radiata</i> <i>rigida</i> <i>serotina</i> <i>virginiana</i>	<i>engelmannii</i> <i>jeffreyi</i> <i>lambertiana</i> <i>ponderosa</i> <i>resinosa</i>	<i>elliottii</i> var. <i>elliottii</i> <i>monticola</i> <i>pinaster</i> <i>strobus</i> <i>sylvestris</i> <i>taeda</i>
Mature height (m)	20 \pm 3	31 \pm 3	29 \pm 3	53 \pm 8	45 \pm 6
Maximum age (yr)	457 \pm 67	217 \pm 44	120 \pm 17	405 \pm 63	285 \pm 35
Growth rate (scale: 1–3)	1.0 \pm 0.0	1.7 \pm 0.7	2.0 \pm 0.2	1.4 \pm 0.2	2.3 \pm 0.2
Reproductive age (yr)	27 \pm 3	15 \pm 3	9 \pm 2	28 \pm 9	10 \pm 1
Reproductive interval (yr)	14 \pm 10	4 \pm 1	2 \pm 1	4 \pm 1	5 \pm 1
Cone length (cm)	7 \pm 1	13 \pm 4	7 \pm 1	20 \pm 7	16 \pm 3
Seed weight (mg)	221 \pm 48	55 \pm 22	13 \pm 2	82 \pm 38	22 \pm 3
Wing length (mm)	0.5 \pm 0.2	2.8 \pm 0.6	1.7 \pm 0.2	2.4 \pm 0.2	2.2 \pm 0.2
Ratio of wing-length/seed wt	0.01 \pm 0.01	0.06 \pm 0.01	0.17 \pm 0.02	0.07 \pm 0.03	0.11 \pm 0.01
Bark thickness (cm)	1.7 \pm 0.2	3.2 \pm 0.3	2.9 \pm 0.5	6.2 \pm 0.7	3.2 \pm 0.1
Self-pruning (scale: 1–10)	1.9 \pm 0.6	6.7 \pm 1.7	2.4 \pm 0.4	8.8 \pm 0.7	6.5 \pm 1.0
Grass stage (% of species)	0	100	0	0	0
Serotiny (% of species)	0	0	92	0	0
Resprouting (% of species)	0	0	46	0	0

^a According to the taxonomic treatment accepted for this volume (Chap. 2, this volume), *P. quadrifolia* Parlatore ex Sudworth is a hybrid between *P. juarezensis* and *P. monophylla*.

Table 12.3. Component loadings for principal components analysis of 13 life-history characters (see Appendix 12.1; WLXSW = wing length/seed weight) for the 38 *Pinus* taxa presented graphically in Fig. 12.21. Components 1 and 2 explained 28.8% and 24.2% of variance, respectively

Life history characters	Component 1	Component 2
WLXSW	-0.830	0.148
SEROTIN	-0.823	-0.148
MAXAGE	0.770	-0.044
MINAGE	0.769	-0.081
SEEDWT	0.618	-0.490
RESPROUT	-0.602	-0.030
GRATE	-0.508	0.384
PRUNE	0.346	0.814
HEIGHT	0.142	0.770
WINGL	-0.268	0.764
BARK	0.181	0.741
CONLENG	0.417	0.704
GRASS	0.146	0.199
INTERVAL	0.195	-0.174

genus, wing size increases and wind-dispersal capacity increases with seed mass, up to about 90 mg, after which further increases in mass are correlated with a decline in wind dispersal capacity. This reflects the qualitative shift from wind to bird dispersal, and these seed character-

istics may have been selected for by nutcrackers and pinyon jays. However, evolution of the very large seed could have other origins, i.e. establishment under extreme temperatures and drought might select for large seeds (e.g. Baker 1972; Fig. 12.20). If true, this would explain the apparent 'loss' of the seed wing, because wings sufficient to carry these large seeds would require extraordinarily large cones (a conclusion drawn from the fact that the two largest seed wings are found in *P. coulteri* and *P. lambertiana*, which happen to have the largest cones in the genus). Alternatively, wind dispersal might have been selected against on these very windy sites where wind dispersal might result in much of the seed crop being lost to unfavourable sites. If aridity and/or wind selected for large wingless seeds, this of course would put a high premium on the coevolution of a bird-dispersal mutualism.

Squirrels may also have affected cone structure in these otherwise bird-dispersed pines. In mountain ranges where squirrels are present, *P. albicaulis* allocates a far greater proportion of energy to protection in the form of a thicker seed coat, and greater cone and resin mass (Benkman 1995a).

12.4.2 Environments with predictable stand-replacing fires

Species in these environments group separately from all other species on axis 1 (Fig. 12.21). The preponderance of serotinous and resprouting species is not surprising, although the lack of these adaptations in other fire regimes is noteworthy (Table 12.2). Thin bark in these fire-type pines reflects the low probability of surviving high-intensity fires. The very short juvenile period and short lifespan were probably selected for by the low to moderate fire-return interval. It may be that these life-history traits are correlated with allometric patterns of biomass allocation to foliage versus structural organs (Strauss & Ledig 1985). Alternatively, features such as short lifespan and poor self-pruning may have been selected to enhance flammability and increase probability of stand-replacing fires (Bond & Midgley 1995). Low seed weight would contribute to greater numbers of seeds, which could be adaptive in light of the fact that seeds are exposed to predators for many years, plus these smaller prey items would reduce feeding efficiency. Other attributes of low seed mass, such as higher wind dispersability, seem less important in relation to the dispersal strategy which is temporal rather than spatial. On the other hand, these pines do have the highest ratio of wing length/seed weight, suggesting high wind dispersability. This may have been selected because stand-replacing fires are likely to generate a vast area of suitable habitat at the time of seed dispersal. Moderate armature and numerous small cones reflects the selective pressure of predation on the constantly available canopy seed source. Predation may also account for annual to biennial cone production.

12.4.3 Environments with predictable ground fires or stand-thinning fires

Species adapted to light ground fires can survive with moderately thick bark and self-pruning (Table 12.2). These environments present a potential threat to seedling survival and thus the evolution of the grass stage in several species is noteworthy; however, some pines persist in such pine savannas without this adaptation.

As site productivity increases, the closed canopy reduces the herbaceous understorey – as well as pine recruitment – and increases the woody fuels that lead to sporadic flare-ups and localized stand-thinning. Increased fire intensity has selected for thicker bark, greater self-pruning, taller stature, larger denser cones, and longer lifespans (Table 12.2). Most pines in these fire regimes are on relatively arid sites and this may account for the significantly greater seed weight than in pines subjected to predictable stand-replacing fires. High seed mass in turn would select for large cones; however, high seed-predator populations are likely to be maintained in these

productive environments, selecting for well-armed cones (McCune 1988). On average, the potential wind dispersability of these pines is not great; however, rodent seed predators appear to play a major role in dispersing and planting these seeds. Additionally, localized flare-ups potentially generate suitable seed beds in proximity to seed source trees, minimizing pressure for long-distance dispersal.

Moderately frequent fires require that saplings reach sufficient size to tolerate repeat fires at a relatively young age. The long juvenile period is consistent with allocation of resources to vegetative growth early in development. These allocation patterns are reflected in far less foliage/structure ratios in these species, as noted by Strauss & Ledig (1985) for *P. jeffreyi* and *P. lambertiana*. The high allocation of resources to protection from fire, and the low probability of crown fires, have selected for long lifespans.

12.4.4 Environments with unpredictable stand-replacing fires

Productive sites where fires are infrequent produce a fire regime of unpredictable high-intensity stand-replacing crown fire (Fig. 12.1). Life-history attributes are most similar to pines adapted to predictable stand-thinning fires (Fig. 12.21; Table 12.2). This suggests that moderately thick bark and self-pruning may occasionally be rewarded. Since the fire-return interval may exceed the lifespan of species such as *P. strobus*, and other more localized types of disturbance may be more frequent than fire, these pines are largely dependent upon wide spatial dispersal of seeds. Tall stature and high wing length/seed weight ratio would be of selective value (Table 12.2). Lack of cone armature on relatively large cones is surprising in these highly productive environments with high seed-predator populations. However, predation may be reduced by long intervals between mast cone years. High growth rate and short juvenile period reflects selection in the face of the rapid colonization by more shade-tolerant broadleaved competitors and the better growth conditions on highly productive sites. Shade tolerance (relative to other pines) may reflect the strategy of maintaining a 'seedling bank', which could take advantage of disturbances other than fire, e.g. windthrows, snowfall, hurricanes etc.

12.4.5 Environments not considered

Not all pine species will fall clearly into one of these life-history modes, but in accordance with niche packing theory, we should expect species intermediate to one or the other of these groups. Two other factors will come into play. Some species are very widespread and encounter more than one fire regime. Also, over time, fire regimes change (e.g. Clark 1989) and adaptations at one point in time may not reflect the selective environment at the time

of origin. Changes in distribution will occur far more rapidly than changes in life history and thus sorting out the life history evolution for narrow endemics, which were once widespread under a different climatic regime (e.g. *P. torreyana*) may be impossible. It is to be expected that over time, species distribution will expand and contract as its suite of traits fits the frequency of adaptive peaks and valleys in the landscape.

In conclusion, we argue that life-history evolution in pines is best understood by relating structural and functional characteristics to site productivity and fire-return interval and these parameters have more explanatory power than models based on fire alone (Rowe 1983;

Landers 1991), or on *r*- and *K*-selection (Caswell 1982, Turner 1985, Strauss & Ledig 1985), competition for light (Govindaraju 1984), moisture requirements (Yeaton 1978, 1981), or plant defence (Loehle 1988).

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Pinus taxa	Firereg	Height	Grate	Maxage	Minage	Interval	Coneleng	Seedwt	Wingl	Grass	Resprout	Serotin	Bark	Prun
<i>albicaulis</i>	N	33	1.0	500	25.0	4.0	5.715	127	0.0	1	1	1	1.270	1
<i>aristata</i>	N	15	1.0	723	20.0	102.0	8.255	20	1.524	1	1	1	1.575	1
<i>balfouriana</i>	N	19	1.0	700	20.0	5.5	10.160	27	2.540	1	1	1	1.575	2
<i>cembra</i>	N	23	1.0	700	27.0	8.0	8.0	413	0.0	1	1	1	1.0	1
<i>cembroides</i>	N	8	1.0	300	25.0	6.5	4.445	350	0.0	1	1	1	1.270	1
<i>edulis</i>	N	12	1.0	350	50.0	3.5	5.080	239	0.0	1	1	1	1.575	1
<i>flexilis</i>	N	25	1.0	300	30.0	3.0	16.510	103	0.0	1	1	1	3.810	7
<i>monophylla</i>	N	15	1.0	150	22.5	1.5	5.080	379	0.726	1	1	1	1.905	1
<i>quadrifolia</i> ^a	N	9	1.0	250	15.0	3.0	5.080	379	0.254	1	1	1	1.524	2
<i>sibirica</i>	N	40	1.0	600	30.0	5.5	7.620	175	0.0	1	1	1	1.651	2
<i>elliottii</i> var. <i>densa</i>	G	26	3.0	150	10.0	3.0	10.795	31	2.540	10	1	1	3.048	5
<i>merkusii</i>	G	31	1.0	200	15.0	1.5	7.620	34	1.900	10	1	1	3.810	5
<i>palustris</i>	G	37	1.0	300	20.0	6.0	20.320	99	3.810	10	1	1	2.794	10
<i>attenuata</i>	R	15	3.0	87	6.5	1.0	11.430	16	3.175	1	1	1	0.965	1
<i>banksiana</i>	R	31	1.0	80	9.0	3.4	4.445	4	0.838	1	1	1	1.270	1
<i>bruta</i>	R	31	2.0	150	8.5	1.0	8.890	28	1.800	1	1	1	4.445	2
<i>clausa</i>	R	25	2.0	60	5.0	1.5	6.858	6	1.524	1	1	1	1.016	1
<i>contorta</i> subsp. <i>latifolia</i>	R	46	1.0	120	7.5	1.0	3.505	5	1.270	1	1	1	1.016	1
<i>echinata</i>	R	31	3.0	200	12.5	6.5	5.080	10	1.270	1	10	1	2.083	4
<i>halepensis</i>	R	25	2.0	150	17.5	1.0	8.890	22	1.400	1	1	1	3.810	3
<i>leophylla</i>	R	25	1.0	300	29.0	3.0	4.445	11	0.838	1	10	7	6.985	6
<i>pungens</i>	R	19	1.0	80	5.0	2.0	7.620	13	2.540	1	10	10	1.905	4
<i>radiata</i>	R	46	3.0	85	7.5	1.0	12.700	28	1.905	1	7	10	4.445	2
<i>rigida</i>	R	31	3.0	100	3.5	6.5	6.350	7	2.540	1	10	10	3.048	3
<i>serotina</i>	R	25	1.0	87	7.0	1.0	5.715	8	1.905	1	10	10	1.575	1
<i>virginiana</i>	R	31	1.5	100	5.0	1.0	5.715	9	0.762	1	10	10	1.270	2
<i>engelmanni</i>	T	25	1.0	400	29.0	3.5	14.986	31	2.540	1	1	1	4.445	7
<i>jeffreyi</i>	T	55	1.0	400	8.0	3.0	25.400	114	2.540	1	1	1	7.620	10
<i>lambertiana</i>	T	69	2.0	425	60.0	4.0	45.720	217	2.540	1	1	1	6.985	10
<i>ponderosa</i>	T	71	1.0	600	18.0	3.5	10.795	38	25.40	1	1	1	7.620	10
<i>resinosa</i>	T	46	2.0	200	22.5	5.0	4.826	9	1.702	1	1	1	4.445	7
<i>elliottii</i>	U	31	3.0	200	8.5	3.0	10.795	31	2.540	1	1	1	3.048	5
<i>monticola</i>	U	62	2.0	400	13.5	5.0	24.130	17	2.540	1	1	1	3.175	7
<i>pinaster</i>	U	37	2.0	250	12.5	4.0	25.400	30	2.300	1	1	1	3.175	6
<i>strobus</i>	U	67	2.0	325	7.5	6.5	15.240	17	2.540	1	1	1	3.175	3
<i>sylvestris</i>	U	40	2.0	350	10.0	5.0	7.620	10	1.100	1	1	1	3.175	10
<i>taeda</i>	U	34	3.0	187	7.5	8.0	10.795	25	1.905	1	1	1	3.505	8

^a According to the taxonomic treatment accepted for this volume (Chap. 2, this volume), *P. quadrifolia* Parlatore ex Sudworth is a hybrid between *P. juarezensis* and *P. monophylla*.

Appendix 12.1. Raw data for 38 pine species used in principal components analysis shown in Fig. 12.21. Firereg = fire regime (codes defined in Table 12.2); Height = metres; Grate = relative growth rate (1=slow, 3 = rapid); Maxage = maximum age (years); Minage = minimum age (years); Interval = period between significant cone crops (years); Coneleng = cone length (cm); Seedwt = seed weight (g); Wingl = seed wing length (cm); Grass = seedling grass stage development (1 = absent, 10 = well-developed); Resprout = relative resprouting capacity (1 = absent, 10 = well-developed); Serotin = degree of cone serotiny (1 = absent, 10 = well-developed); Bark = bark thickness (cm); Prun = relative self-pruning capacity (1 = absent, 10 = well-developed).