Chapter 12

Seedling communities

Jon E. Keeley and Phillip J. van Mantgem

12.1 Introduction

This chapter considers the internal and external processes that affect seedling communities. Internal or endogenous drivers include the density dependence of seedling populations as well as the relationship of parent to offspring and the competitive relationships affecting seedling populations. There are many external or exogenous drivers, but we will focus on climate, predation, and fire. We will integrate these internal and external drivers of community composition to address the questions: To what extent do seedling recruitment strategies relate to community assembly rules and do these rules dictate the potential combinations of regeneration niches to be found in any given community? This chapter will focus on long-lived woody species because the differences in life history stages and factors affecting them appear much more prominent than in some other growth forms.

12.1 Internal drivers

Communities of regeneration niches

Plant recruitment strategies have received a great deal of attention generally to determine the environmental conditions that favor one strategy over another (Chapter 11). Although communities comprise an assemblage of different seedling strategies, relatively little attention has been paid to the community combinations or rules that limit possible combinations. A useful concept for understanding seedling communities is that of safe sites (Harper, 1977), which is a species-specific phenomenon driven by unique aspects of ecology and phylogeny. It is important to recognize the diversity of potential safe sites and how they are distributed in space and time. Also of importance is how species reach safe sites and the role of metapopulations.

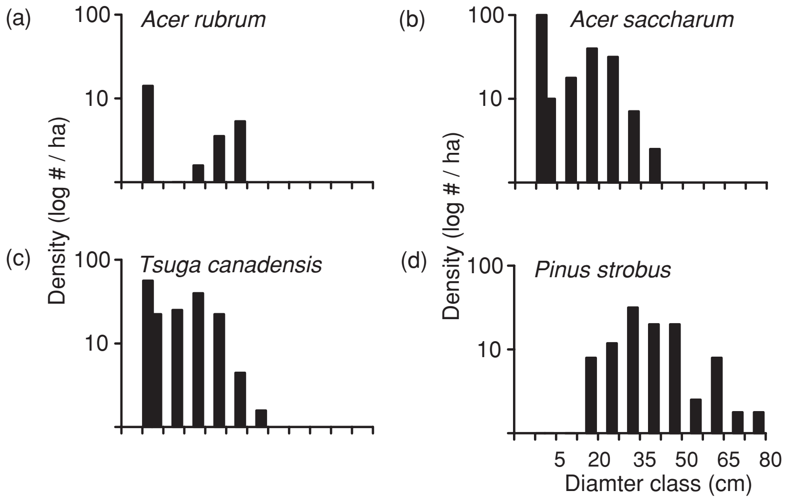

Fig. 12.1 Size structure of dominant tree species in a mid-western North American (Wisconsin, USA) *Acer saccharum* forest. Redrawn from Goff & Zedler (1968).

Plants differ in three important ways in reaching safe sites, which they accomplish by dispersal, seed dormancy, and delayed growth. All three of these may be utilized by the same species, but here we will focus on three functional types that represent modes in a continuum. *Spatial dispersers* reach safe sites that are widely distributed in space although potentially available every year. *Temporal dispersers* have innate or enforced seed dormancy that delays germination until conditions are suitable for generating the appropriate safe sites. These sites may occur annually in the appropriate season for some species or occur periodically following disturbance. *Persistent seedling banks* represent safe sites for seedling recruitment, but require a change in conditions for recruitment into the adult population, something foresters often refer to as *advanced regeneration*. An example in forests would be a pool of seedlings and saplings that opportunistically recruit into the overstory as canopy gaps occur. This is explicit in gap models of forest dynamics (JABOWA and its descendants), where recruitment is wholly dependent on canopy gap availability, size, and arrangement (Bugmann, 2001). Seedling banks that persist in the understory grow slowly, but this provides sufficient advantage for successful recruitment into the canopy when gaps finally occur (e.g. Brown & Whitmore, 1992).

Plant population biology has been concerned with discerning those environments that select for one strategy or another. Here we focus on the seedling community and ask to what extent these strategies coexist and whether there are patterns in the combinations of strategies and their temporal and spatial dispersion.

In North American deciduous forests, seedling communities comprise temporally separated recruitment patterns that illustrate these strategies (Fig. 12.1). *Pinus strobus* (Pinaceae), although a dominant in this forest, lacks seedling recruitment in the understory as it is dependent on disturbances, which apparently have not occurred for some time. Large stand-replacing fires favor recruitment of this species if a nearby seed source exists, however, lighter understory burns may favor recruitment as well (Holla & Knowles, 1988). To recruit, *Pinus strobus* must disperse spatially until a propagule lands on a suitable open site. *Tsuga canadensis* (Pinaceae) and *Acer saccharum* (Aceraceae) recruit continuously, and these are successfully recruited into larger size classes (Hett & Loucks, 1971). *Acer rubrum* exhibits a very different strategy with recruitment occurring continuously, but in the absence of canopy gaps, seedlings fail to develop further. Seedling banks in this species accumulate because shaded understory conditions produce a favorable environment for drought-sensitive seedlings, but recruitment into the canopy requires higher light (Lambers & Clark, 2005). However, not all gaps are suitable for recruitment (Royo & Carson, 2006). Beckage *et al.* (2005) found that dense understory shrubs limit recruitment in small canopy gaps for *Acer rubrum*. They further found that variability in seedling survivorship was seven times greater across time than space, that is, temporal variability was much greater than the effect of light gaps, suggesting the difficulty in precisely defining safe sites for all populations of a species.

Although these seedling/sapling establishment patterns observed for this deciduous forest (Fig. 12.1) imply species-specific differences in recruitment, this is based on the community structure only at a single point in time and misses much complexity. In contrast, if we examine annual patterns of seedling community dynamics over an extended period, we find that recruitment strategies may vary from year to year. Seedling communities for the dominant trees in a mixed-conifer forest in western North America (California, USA) over a period of eight years illustrates marked annual changes (Fig. 12.2). In the year 2000, the major seedling recruitment was for *Abies concolor* (Pinaceae) and *Calocedrus decurrens* (Cupressaceae), with little contribution from *Pinus ponderosa*. However, if we were to examine this community in 2004, we would see a different picture with substantial recruitment by *P. ponderosa* and relatively few new seedlings of the other two species. These pine seedlings apparently did not persist into older age classes, unlike *A. concolor* and *C. decurrens*. *Quercus kelloggii* (Fagaceae) has modest recruitment each year and these recruits persist well into the older age classes ($\geq$3 yrs).

Other forest types also exhibit spatial and temporal variation in seedling communities (e.g. Houlé, 1992, 1994). For example, based on size structure, *Acer saccharinum* in midwestern North American forests (Wisconsin, USA) appears to recruit successfully into the canopy of undisturbed forests (Fig. 12.1) (Goff & Zedler, 1968), yet in eastern North American forests, this species maintains seedling banks dependent on canopy gaps (Marks & Gardescu, 1998). Likewise, *Tsuga* species recruit in the forest understory as suggested by Fig. 12.1, but may also exhibit increased recruitment around the edges of gaps not exposed to direct solar radiation (Gray & Spies, 1996). *Tsuga canadensis* and

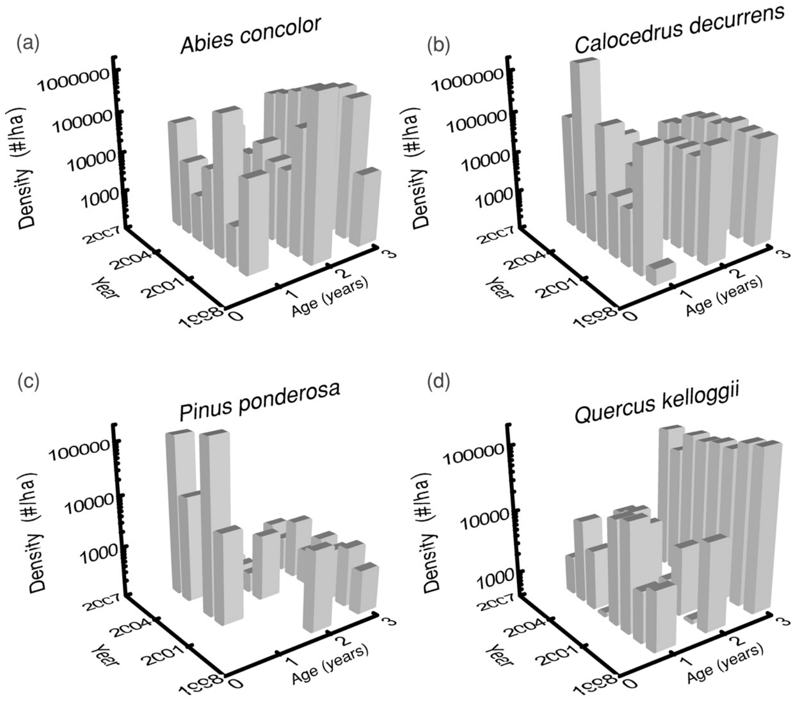

Fig. 12.2 Seedling populations for 1-, 2- and ≥3-yr-old seedlings of the dominant trees in a western North American mixed conifer forest in the southern Sierra Nevada (California, USA). Keeley, van Mantgem & Stephenson, unpubl. data.

Acer saccharum with similar temporal patterns of seedling recruitment also demonstrate similar microhabitat preferences (Goff & Zedler, 1968).

Within communities seedling recruitment often exhibits marked spatial variation in response to microhabitat gradients. For example, in the oak-pine forest of the New Jersey Pine Barrens (USA), first-year seedling recruitment by six dominant species exhibited significant spatial variation in their preferences for litter depth, moss cover, lichen cover, percentage canopy cover, and nearest neighbor distance (Collins & Good, 1987). Also, as resources change along gradients, competition may change and alter the favorability of sites for seedling establishment (Boerner & Brinkman, 1996; Davis *et al.*, 1998; Catovsky & Bazzaz, 2002). In communities where there is marked temporal and spatial variation in patch favorableness, it has been suggested that this hinders populations from reaching a stable spatial distribution and a stable age distribution with a fixed schedule of recruitment and mortality within a patch (Fowler, 1988).

In many forest types, fire has a profound effect on seedling recruitment and the timing of such events can have important impacts on species that commonly have periodic mast years of seed production. In mixed conifer forests of the southern Sierra Nevada (California, USA), *Abies concolor* typically produces a mast year every 2–3 years (Fowells,

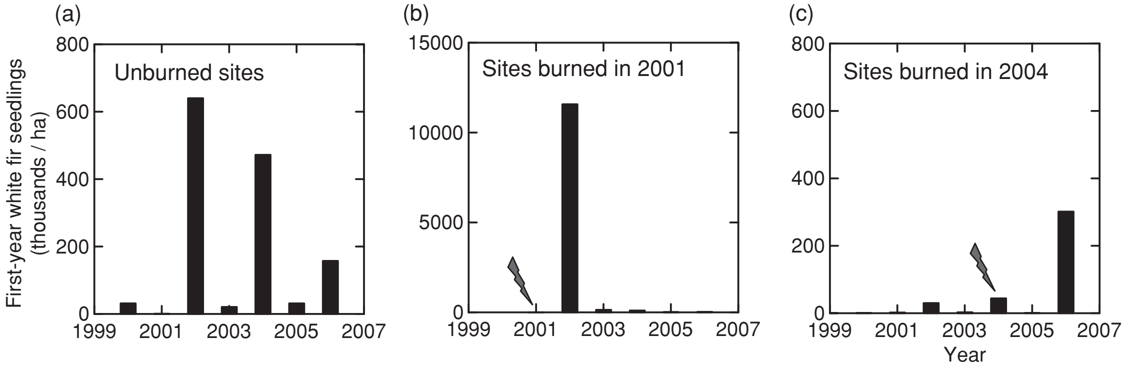

Fig. 12.3 First year *Abies concolor* seedlings in (a) unburned sites, n = 11 one or two-ha sites with average density of 376 trees per ha; (b) sites burned in 2001, one year prior to a mast year, n = 3 sites with average density of 314 trees per ha; and (c) sites burned in 2004, two years prior to a mast year, n = 2 sites with average density of 61 trees per ha. Sites were in *Abies concolor* dominated forests in Sequoia National Park (California, USA). Arrow represents fire year. Keeley, Stephenson & van Mantgem, unpubl. data.

1965) and historically these forests have been prone to surface fires every decade or two (Caprio & Lineback, 2002). The timing of mast year events relative to fire events is likely to affect seedling recruitment and there is some evidence of this effect in Fig. 12.3. Burning followed immediately by a mast year of seed production (Fig. 12.3b) provides more resources for seedling recruitment than a mast year delayed two years after burning (Fig. 12.3c). In the former case, seedling recruitment is many times greater than in the latter case. This appears to be a widespread phenomenon occurring in different forest types and this interaction between fire and masting cycles has been shown to have long-lasting impacts on forest demography in northern (Alberta, Canada) *Picea glauca* forests (Peters *et al.*, 2005).

Internal dynamics

Obviously, persistence of ecological communities requires reproduction, however, there has not been widespread agreement on the role of regeneration dynamics in determining community composition and structure. Influenced by equilibrium concepts of communities, some see regeneration as the mechanism that maintains community composition and structure, and this is ultimately determined by traits of mature plants. In contrast, others, influenced by the growing appreciation for disequilibrium processes, see community composition and structure as determined heavily by regeneration processes.

Some of the differences in these two approaches center on a different evaluation of the importance of competition as a factor in structuring communities (Howard & Goldberg, 2001). Where competition is a key force, it is often most intense in the adult stage and of lesser importance in seedling communities (Poore, 1964). In forests, competition has long been regarded as a primary driver determining community structure and regeneration dynamics has not been generally seen as critical to determining either composition or structure (size and spatial arrangements of stems) of the overstory community (Swaine & Hall, 1988). Instead, regeneration processes are often thought to be dependent on the availability of sites suitable for overstory recruitment, usually canopy gaps, that provide sufficient resources for recruitment into the canopy. This view is supported by the fact that forest gap models are able to recreate forest communities successfully, although many of the mechanisms proposed by these models are difficult to test independently (Prentice *et al.*, 1993; Bugmann, 2001). As long as processes such as regeneration are not well understood, these models may produce the predicted forest communities, but for the wrong reasons.

There is an emerging view, however, that regeneration processes, that is, seed production (fecundity), seed dispersal, seed germination, and seedling survival and growth, may limit populations of many, if not most, forest tree species (Veblen, 1986; Clark *et al.*, 1999). Thus, community composition and structure may, in part, be determined by regeneration processes. This is suggested by lowland tropical forest diversity patterns that show seedling diversity is a subset of diversity in the adult community, setting the community on a new trajectory (Comita *et al.*, 2007). A multitude of factors control the regeneration process, but at the seedling stage, competition with other growth forms, such as herbaceous effects on tree seedlings, often greatly impact recruitment success (Maguire & Forman, 1983; Meiners & Handel, 2000). In some environments, coexistence of competitively similar species may result from differences in timing and success of seedling recruitment and are predicted by lottery models of recruitment (Bond & van Wilgen, 1996). Of particular importance are recruitment limitations that lessen the effect of competitive asymmetries between dominants and this may contribute to coexistence and greater community diversity (Hurtt & Pacala, 1995).

Thus, a critical question in community ecology is, what life history stage is most critical in determining community structure and distribution? Put another way, is selection operating more on the regeneration niche (*sensu* Grubb, 1977) or the adult niche (Reich, 2000)? This has been studied by examining the relationship of species occurrence along environmental gradients for seedlings, saplings, and adults (Stohlgren *et al.*, 1998; Collins & Carson, 2004; Chapter 10). In some cases, seedling distribution shows a much broader distribution than adults and in other cases it does not (Fig. 12.4). Interpreting these patterns, however, requires consideration of site history and past climates. For example, in the absence of such information, one might interpret that the distribution of *Quercus rubra* arises from limited tolerance of adult trees and this restricts them to a narrow subset of sites, despite the larger tolerances of seedlings and saplings (Fig. 12.4a). However, past site history of logging or climate changes could account for their present restricted distribution while the wider distribution of seedlings could indicate a new trajectory for the future distribution of this species (Collins & Carson, 2004). The

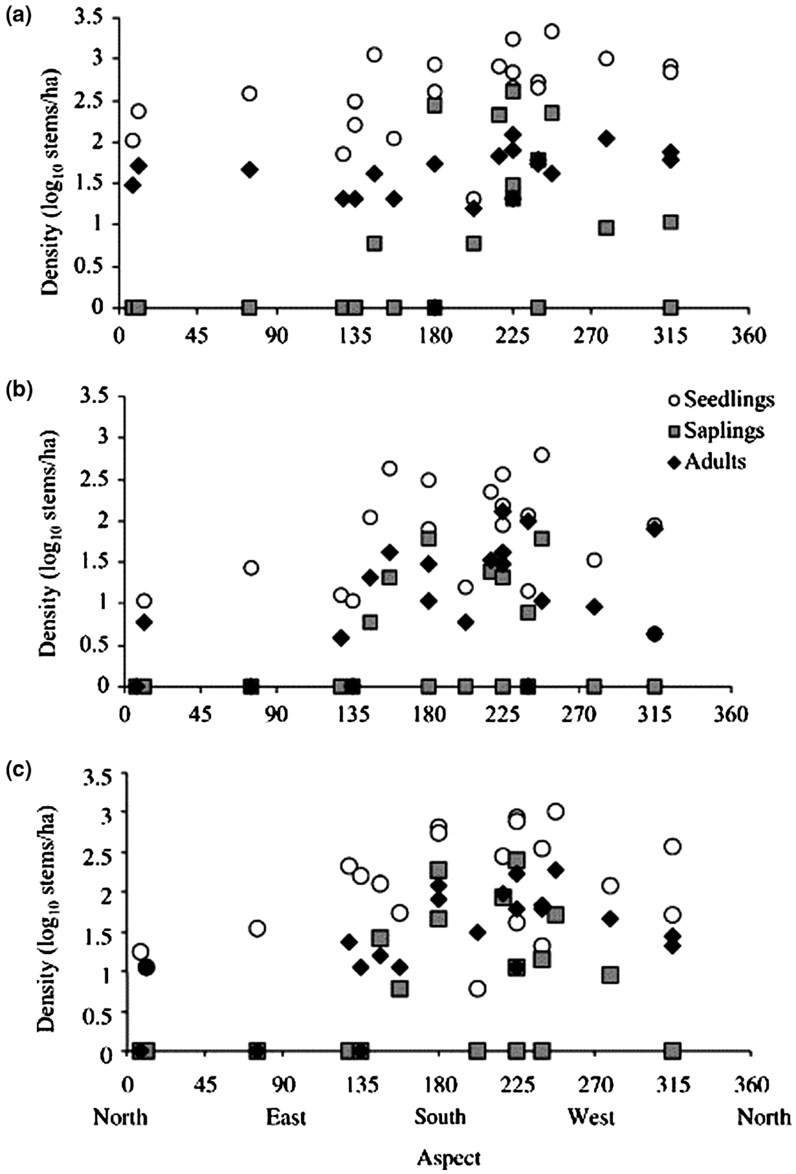

Fig. 12.4 Stem density for seedlings, saplings and adults across different slope aspects for (a) *Quercus rubra*, (b) *Q. alba*, and (c) *Q. prinus* in an eastern North American (USA) deciduous forest. From Collins & Carson (2004), reprinted with permission from Elsevier.

opposite is possible as well, where adult trees are more widely distributed than seedlings and saplings due to land use changes such as fire exclusion from fire-prone environments, which alters site favorability for recruitment (Parsons & DeBenedetti, 1979; Rooney *et al.*, 2000).

The recruitment strategies of certain chaparral shrubs provide an example of where distributions are more a function of adult traits and seedling recruitment is, thus, largely controlled by adult traits. Species differ in their mechanisms for dealing with drought stress in the semi-arid region of coastal southwestern North America (California, USA). Some species have physiological tolerances to drought and others morphological traits to help avoid drought stress. These mechanisms constrain options available to seedlings and enforce a very narrow range of conditions under which recruitment is successful (see Box 12.1).

Box 12.1 Factors determining seedling dynamics in the fire-prone chaparral shrublands

Several dominant species recruit only on open sites in the first postfire year, whereas others only recruit under the canopy during fire-free periods. In postfire recruiters such as *Adenostoma fasciculatum*, soil-stored seeds are dormant and seedling cohorts occur in a single pulse after fire. *Rhamnus crocea* has transient seed banks leading to recruitment in the understory during fire-free periods and age structure studies show these successfully recruit into the overstory canopy (Keeley, 1992). In others, such as *Quercus berberidifolia*, seed banks are also transient, but seedlings are rare except in the long-term absence of fire (several decades), apparently because of the requirement for shade and deep organic soil. Herbivory of these seedlings or saplings is intense, but they persist in a suppressed form due to resprouting from the base and successful recruitment into the canopy often requires a fire that provides better growing conditions for the resprouting saplings.

This temporal separation of seedling populations does not appear to be tied to selection for avoidance of competitive interactions in seedling communities, but rather to a suite of traits that are the necessary outcome of differences in how adult populations survive in these semi-arid environments (Keeley, 1998). They are correlated with character syndromes involving physiology, morphology, and other reproductive traits. The postfire recruiting species are capable of tolerating drought with physiological and morphological traits that allow them to persist under extreme water stress. These traits confer on seedlings the ability to tolerate the intense drought stress characteristic of open burned sites and thus the ability to recruit after fire when resource conditions of light and nutrients are highly favorable. Mature shrubs of the fire-free understory recruiters have a much weaker tolerance of water stress, but have deep root systems that can access underground water sources unavailable to the more shallow rooted fire recruiter species. This avoidance strategy works well for established shrubs, but is not an option for their seedlings that require many years' growth to develop root systems sufficient to tolerate conditions on open burned sites. As a consequence, seedling recruitment is restricted to the deep shade under the shrub canopy and to old growth stands with deep litter and duff, which retain moisture longer into the summer drought. In this respect, these shrub species have a similar seedling recruitment pattern to *Tsuga* spp. that recruit in old growth forests and are often dependent on substrates with sufficient decaying wood having greater moisture-holding capacity than mineral soil (e.g. Turner & Franz, 1985; Marx & Walters, 2006). Other less known examples of species with seedling recruitment restricted to moist and dense litter microhabitats also have been noted (Williams *et al.*, 1990). Similar seedling avoidance of canopy gaps and restriction to shaded mesic understory sites is seen in some tree species in semi-arid forests of the Mediterranean Basin (Espelta *et al.*, 1995; Gómez-Aparicio *et al.*, 2005).

Correlated with these seedling recruitment modes are very different fruit and seed characteristics. The postfire seeding species are temporal dispersers with weakly developed dispersal and deeply dormant seeds requiring fire cues for germination, a sort of sit and wait strategy. The fire-free understory recruiters have fleshy fruits that are animal dispersed and these transient seed banks fail to accumulate in the soil. These character syndromes also have a biogeographic and phylogenetic component. Fire recruiters appear to represent more restricted taxa that have radiated relatively recently, perhaps in response to the increasing importance of fire in the late Tertiary (Keeley & Rundel, 2005). The fire-free recruiters are widespread in the Northern Hemisphere and appear to be much older lineages that persist in micro-habitats that have been present throughout the late Tertiary (Keeley, 1998).

Thus, we interpret the seedling community dynamics of this shrubland as a reflection of very different strategies for handling water stress and the marked temporal separation in recruitment patterns to be a necessary part of the character syndrome of drought avoiders and drought tolerators. Similarly, one might argue that the *Acer saccharum* forest community of seedling recruitment patterns is tied to life history trade-offs in shade-tolerance strategies for the adult population (Curtis, 1959), and these appear to be tied to different patterns of seed dispersal and persistence (Houlé, 1991, 1994).

On the other hand, one of the clearest examples where seedling recruitment requirements dictate community composition is in riparian trees. Adult *Salix nigra* (Salicaceae) distribution, for example, is unaffected by factors such as soil moisture, aeration, and nutrients, but seedling recruitment is strictly limited by these factors (McLeod & McPherson, 1973). Thus, it appears that mature trees could survive in a much broader range of environmental conditions than those to which they are restricted because of seedling requirements, and this may generally be the case with riparian species (Sacchi & Price, 1992). Similarly, the distribution of savanna and forest species is apparently constrained by seedling characteristics that differ in tolerance to frequent burning (Hoffmann, 2000). Tropical rain forest communities provide a very compelling case for the importance of the regeneration niche. Across a range of species, the physiological and morphological leaf traits of seedlings, saplings, and adults were most strongly correlated with the crown exposure at the regeneration stage (Poorter, 2007).

Thus in some cases, community composition and structure is determined by characteristics of adult populations and in other cases by characteristics of seedling populations. A third pattern is the potential for adult populations to modify their environment in ways that promote seedling recruitment, a process termed *niche-construction* (Odling-Smee *et al.*, 2003). One such example is in mast flowering bamboos, which have the unusual characteristic of dying *en masse* after setting seed. It has been hypothesized that in these high light-demanding forest bamboo species mortality alters the environment by creating a massive fuel load that promotes burning and enhances conditions for seedling recruitment (Keeley & Bond, 1999, 2001; but see Saha & Howe, 2001).

Impacts at larger scales

If recruitment limitation has the potential to influence forest communities, it raises the question of how these processes might affect communities on a broader scale. Specifically, are there patterns in the effect size of recruitment limitations that could give rise to diversity gradients across temperate and tropical forests? The possibility that this might be the case was raised independently by Janzen (1970) and Connell (1971), who argued that density-dependent forces, particularly at the seed and seedling stages, are stronger in tropical than temperate forests, reducing the ability for a particular species to dominate in tropical forests, thereby promoting diversity. Stronger density-dependent effects would arise in tropical forests due to plant enemies, related to the greater abundance of specialist predators and pathogens in the tropics and because adult trees would serve as foci for these enemies. Thus with increasing distance from the parental trees, seeds and seedlings would be further from the enemy population sources and less available to these enemies.

These ideas, known as the Janzen-Connell hypothesis, have been the object of considerable research since they were first proposed. Testing has concentrated in two areas, finding evidence for density-dependent survival in tropical forests and documenting differences in density-dependent effects in tropical compared to temperate forests. Substantial evidence, both in favor of and against strong density-dependent effects in tropical forests, was recently synthesized in a meta-analysis by Hyatt *et al.* (2003). They found no consistent evidence for density dependence for seeds and weak affirmative evidence for seedlings. The search for density dependence in tropical forests remains an active area of research (e.g. Peters, 2003; Bell *et al.*, 2006; Webb *et al.*, 2006). Comparisons of the effect of density dependence in tropical and temperate forests have received relatively little work, although recent papers have demonstrated the presence of strong density dependence of seedlings in temperate forests (Lambers *et al.*, 2002; Reinhart *et al.*, 2005b). Interestingly, there has been little work investigating the mechanisms driving the Janzen–Connell Hypothesis. Moreover, there have been few demonstrations that there is a greater proportion of specialist seed or seedling enemies in tropical than in temperate forests, or that the presence of adult trees modulates visibility to specialist predators (but see Leigh *et al.*, 2004; Freckleton & Lewis, 2006). Furthermore, not all density-dependent effects are negative. For example, oak regeneration may be enhanced by greater mycorrhizal infection when recruiting near rather than far from adult trees (Dickie *et al.*, 2007).

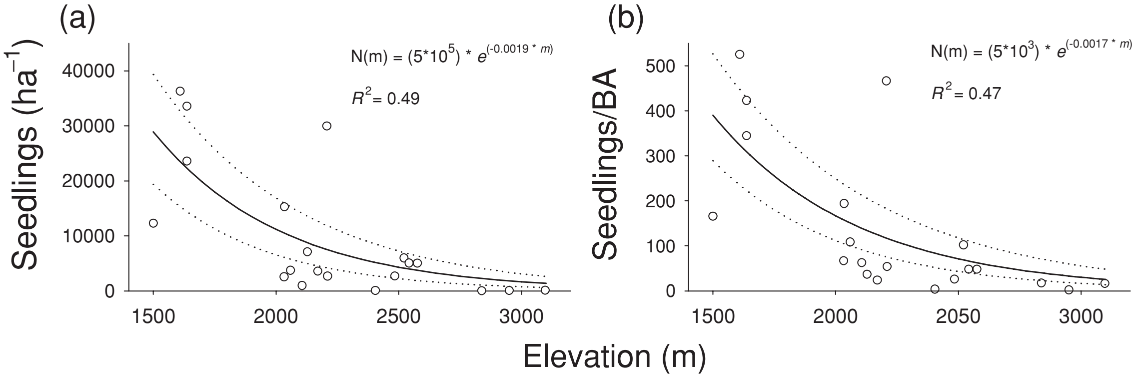

Fig. 12.5 The relationship between elevation and seedling densities across 20 long-term monitoring plots in coniferous forests of the Sierra Nevada (California, USA). (a) Average number of seedlings (ha^{-1}) and (b) average number of seedlings relative to the basal area (m^2 ha^{-1}) of potential parent trees defined as trees within 25 m of the sample plot (b). The solid line is the nonlinear regression estimate, with the dotted lines showing the 95% confidence intervals calculated from 5,000 bootstrapped estimates. N(m) is the number of seedlings at a given elevation and m is the elevation (in meters). From van Mantgem *et al.* (2006), reprinted with permission from Elsevier.

12.3 External drivers affecting seedling communities

Climate

The distribution and dynamics of forest trees are strongly influenced by climate (Stephenson, 1990, 1998; Stephenson & van Mantgem, 2005). These patterns may arise at least in part by the effects of climate on reproduction, known to be sensitive to climate (Fowells & Stark, 1965; Stohlgren *et al.*, 1998; Collins & Carson, 2004; Gworek *et al.*, 2007). For seedlings, climate may determine patterns of seedling recruitment and growth (Olszyk *et al.*, 1998; Castro *et al.*, 2004a). Climate may interact with other factors such as fire, and with species-specific recruitment responses that vary in response to different combinations of factors (North *et al.*, 2005). In general, the limited spatial and temporal scale of most seedling studies (Clark *et al.*, 1999) restricts our understanding of how climate may control their dynamics. This is a particular critical problem in deserts where recruitment may be a rare event (Cody, 2000).

Using a network of long-term seedling monitoring plots, van Mantgem *et al.* (2006) recently showed that seedling densities changed significantly over an elevation (climatic) gradient in the Sierra Nevada Mountains (California, USA) (Fig. 12.5a). The relationship between seedling density and elevation held when potential parent tree basal area was considered (Fig. 12.5b). In this study, *Abies* and *Pinus* species, the two dominant genera in these forests, both showed decreasing seedling densities with elevation, but with a stronger response in *Pinus*. Thus, the seedling response to climate was widespread, but with measurable differences among taxa (Kern, 1996; Green, 2005).

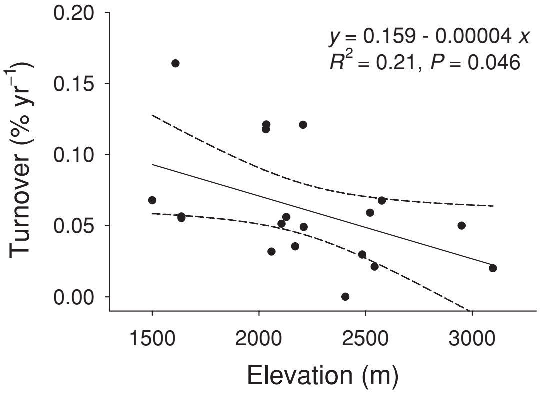

Fig. 12.6 The relationship between elevation and turnover rates (mortality over recruitment) of tagged seedlings (>10 cm tall) from the same forests as in Fig. 12.5. The solid line is the regression estimate with the dashed lines showing the 95% confidence interval. From van Mantgem *et al.* (2006), reprinted with permission of Elsevier.

Additionally, van Mantgem *et al.* (2006) found evidence that turnover rates (the average of recruitment and mortality rates) for tagged seedlings more than 10 cm tall declined with elevation (Fig. 12.6). Because climatic data indicate that site potential for primary production may decrease with elevation in the forested zone of the Sierra Nevada (Stephenson, 1988), a negative relationship between seedling turnover and elevation is consistent with broader patterns of forest overstory productivity (Stephenson & van Mantgem, 2005). However, van Mantgem *et al.* (2006) found that not all phases of reproduction were related to climate, with seed production apparently independent of elevation. The response of seedling densities to elevation may be mediated by a greater proportion of seeds that become successfully established at lower elevations (Fig. 12.7). This finding suggested that spatial variation in early phases of recruitment (e.g. proportion of sound seeds, seed predation, germination, and first-year mortality) may strongly influence patterns of seedling community structure.

Herbivores, predators, and pathogens

Herbivores and granivores are known to affect the composition of seedling communities (Guo *et al.*, 1995; Hanley, 1998) and much work has been done to document their effects as a possible mechanism causing density dependence in the context of the Janzen–Connell Hypothesis (see above). However, one of the clearest illustrations of predation pressure on seeds and seedlings is the presence of mast flowering behavior in many tree species (Kelly & Sork, 2002). Selection for masting cycles of high and low seed years is widely considered to have been driven by seed and seedling predation. The theory argues that a hiatus of one to several years in which seeds and seedlings are in short supply acts to reduce predator populations and mast years satiate predators (Brown & Venable, 1991). One factor working against such a mechanism would be a lack of synchrony with other species

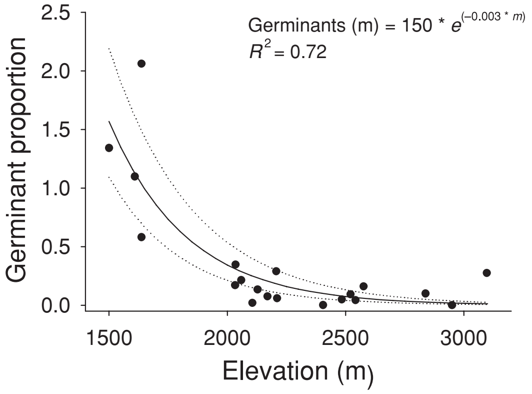

Fig. 12.7 The relationship between elevation and the average proportion of germinants (1st year seedlings at year t+1/seeds at year t) from the same forests as in Fig. 12.5. The solid line is the nonlinear regression estimate, with the dashed lines showing the 95% confidence intervals calculated from 5,000 bootstrapped estimates. This pattern may help explain the relationship between elevation and seedling densities (Fig. 12.5). Note that germinant proportions above 1.0 implies the presence of seed banks, but more likely represents measurement error from combining seed trap counts of seed densities versus plot-based seedling counts. Van Mantgem, Keeley & Stephenson, unpubl. data.

within the community. There is some evidence that congeneric oak species in the same community often are synchronized in seed production (Koenig & Knops, 2002). However, more often communities comprise unrelated taxa that are not synchronous in annual seed and seedling production (e.g. Fig. 12.8). This appears to be the case not only in temperate forests but tropical forests as well (De Steven, 1994).

Escape from pathogens is also sometimes considered as a driver of the evolution of masting behavior (Pearson *et al.*, 1994). In tropical forests, pathogens are known to play a major role in seedling mortality because their presence increases near adult trees (Augspurger, 1984b), and is one of the mechanisms favoring the Janzen–Connell model discussed above.

Herbivores affect seedling communities through direct herbivory and indirectly by predation of flowers and seeds. In many cases, seedlings are far more palatable than adults (Fenner *et al.*, 1999). Species replacements along gradients are often interpreted as due to competitive interactions, but seed predation can also be the driver behind species replacements along different resource gradients (Louda, 1989). In addition, density-dependent effects of herbivory on seedling populations can play a significant role in promoting community coexistence (Hulme, 1996). Landscape patterns may also affect the level of impact. For example, small prescribed burns that are surrounded by unburned vegetation may provide patches of rodent habitat in close proximity to patches of seedling recruitment in burn areas, resulting in much more intense herbivory than observed after large wildfires (Bullock, 1991; Keeley, 2000).

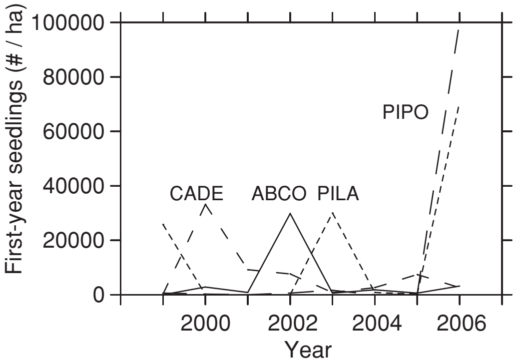

Fig. 12.8 First year seedling populations from 1999 to 2006 for the *Abies concolor* (ABCO), *Calocedrus decurrens* (CADE), *Pinus lambertiana* (PILA), and *P. ponderosa* (PIPO) in a mixed conifer forest in the central Sierra Nevada (California, USA). Keeley, van Mantgem & Stephenson, unpubl. data.

Herbivory and granivory need not always be associated with negative effects on seedling communities. For example, in southwestern North American *Pinus ponderosa* forests, frequent fires are a major consumer of tree seedlings, and grazers represent a potential competitor with fire (Bond & Keeley, 2005). When grazing pressure is intense, fuels fail to accumulate sufficiently to carry fire and establishment success of tree seedlings increases.

Fire

The effect of fire on seedling communities must be considered in the context of fire regimes. Different fire regimes have selected for different seedling recruitment patterns that are affected very differently by burning patterns at the community and landscape levels. A quick overview of woody plant regimes is illustrated by comparing four North American plant communities (USA): southeastern long leaf pine, Sierra Nevada mixed conifer, Great Basin pinyon-juniper woodland, and California chaparral.

Long leaf pine ecosystems in the southeastern USA have one of the highest fire frequencies of any ecosystem due in part to the extraordinary density of summer lightning storms (Glizenstein *et al.*, 1995). The dominant tree, *Pinus palustris*, has bark and self-pruning characteristics that make it relatively resistant to frequent fires. The frequency of fires leads to low fuel loads that result in light surface fires and high survival of dominant overstory trees. *Pinus palustris* seedling populations are dependent on fires to clear surface litter and herbaceous competition and on the overstory survival for seed production. There is little evidence that landscape patterns of burning play a significant role in seedling recruitment.

On the other hand, in some western mixed conifer forests, pattern of burning plays a significant role in seedling recruitment. On these sites, productivity is substantially higher and fuel loads heavier and, as a result, fire regimes comprise a mix of low intensity surface fires that burn in the forest understory and high intensity crown fires that create gaps within the community. These gaps favor seedling recruitment (Mutch & Parsons, 1998; Keeley & Stephenson, 2000) and the distance of gaps from parent seed trees is critical to establishing seedling populations for most of the dominant species.

California chaparral shrublands typically burn in high intensity crown fires that often cover thousands of hectares. Dominants in this ecosystem either resprout from the base or have dormant seed banks that establish even-aged cohorts after fires (Box 12.1). As a consequence, landscape patterns of burning are relatively unimportant to their recovery.

Pinyon-juniper woodland characteristically burns at long intervals in large, high intensity crown fires (Wright & Bailey, 1982). None of the dominants, pinyon (*Pinus* spp), juniper (*Juniperus* spp. Cupressaceae), or sagebrush (*Artemisia tridentata* Asteraceae) have much of a dormant seed bank and, thus, the landscape pattern of burning is critical to recovery because seedling recruitment is dependent upon colonization from unburned patches left on the landscape.

12.4 Seedling community assembly rules

Community assembly rules arise from the concept that if different communities are repeatedly assembled from a common species pool, then there must be rules that constrain community composition. These rules are restrictions based on the presence or abundance of other species and not simply the species-specific response to the environment (Diamond, 1975). The rules are modified by different environmental filters to generate different community composition and different assembly histories may generate multiple stable equilibria (Chase, 2003). Some define assembly rules narrowly as just those patterns due to species interactions (Wilson, 1999). However, because interactions vary as environments change, others consider assembly rules as those patterns resulting from the combination of environmental filters and species interactions (Weiher & Keddy, 1995; Holdaway & Sparrow, 2006).

Because seedlings represent the initial stage of assembly for plant communities, we ask the question, are there assembly rules that determine seedling communities? California (USA) sage scrub provides a useful model system for examining the factors determining seedling community assembly because recruitment is largely centered around fire events and is limited after canopy closure. This semideciduous shrubland is dominated by a variety of growth forms resilient to fires that periodically kill all aboveground biomass. Many herbaceous and woody species maintain deeply dormant seed banks that are fire-stimulated and most woody species are capable of resprouting from underground vegetative parts. In general, seedling communities are restricted to a narrow window of time after fire, but with some variation in the exact timing of recruitment (Table 12.1). For

Table 12.1 Woody species seedling recruitment in California (USA) sage scrub communities during the first 5 years after fire (from Keeley *et al.*, 2006). Included are all woody species present at 10 or more of the 50 sites in this study. The chaparral shrub Adenostoma fasciculatum was a minor component at 11 of these sites, but is not included here because it is not generally considered part of the sage scrub community.

					Total for years 1–5 (#/ha)		Percentage by year				
Species	Plant Family	Fire response[a]	Resprout (%)[b]	Life form[c]	# sites	$\bar{x}$	1	2	3	4	5
First-year seedling pulse:											
Calystegia macrostegia	Convolvulaceae	OS[d]	0	su	34	38,630	92	5	2	0	1
Eriogonum fasciculatum	Polygonaceae	FS	10	ss	32	24,500	71	21	5	0	3
Lotus scoparius	Leguminosae	OS	0	su	43	77,600	72	9	2	1	16
Malachothamnus fasciculatus	Malvaceae	FS	~ 15	ss	25	54,400	93	1	5	1	0
Malosma laurina	Anacardiaceae	FS	95	s	27	3,900	90	8	1	1	0
Rhus integrifolia	Anacardiaceae	FS	74	s	13	800	50	20	0	0	30
Ribes spp.	Grossulariaceae	FS	98	ss	11	20,100	85	6	4	0	5
Salvia mellifera	Lamiaceae	FS	14	ss	25	15,900	73	12	3	3	9
Second-year seedling pulse:											
Encelia californica	Asteraceae	OR	83	ss	11	172,100	0	67	15	0	18
Galium angustifolium	Rubiaceae	OR	99	su	23	40,600	4	55	10	17	14
Hazardia squarrosa	Asteraceae	OR	100	ss	22	49,500	0	54	34	6	6
Mimulus aurantiacus	Scrophulariaceae	FS	46	ss	24	142,800	4	60	16	4	16
Mirabilis californica	Nyctaginaceae	OR	~ 99	su	19	1,900	0	70	29	0	1

Table 12.1 (Cont.)

Multi-year recruitment:											
Artemisia californica	Asteraceae	FS	20	ss	41	31,500	41	42	13	1	4
Eriophyllum confertiflorum	Asteraceae	FS	~ 99	su	30	24,000	20	33	24	10	13
Galium nuttallii	Rubiaceae	FS	~ 99	su	27	27,700	3	32	21	12	32
Lessingia filaginifolia	Asteraceae	OR	~ 99	su	10	47,400	0	41	18	12	29
Rhamnus crocea	Rhamnaceae	OR	100	s	14	300	4	0	15	4	77
Salvia apiana	Lamiaceae	FS	63	ss	14	22,900	23	23	42	10	2
Salvia leucophylla	Lamiaceae	FS	87	ss	10	10,000	46	12	31	1	10
Solanum spp.	Lamiaceae	FS	~ 99	su	23	4,400	40	21	20	4	15

[a] First-year fire response of seeding and vegetative resprouting: OS = obligate seeder, FS = facultative seeder, OR = obligate resprouter;

[b] s = percentage of prefire population resprouting except for those indicated with ~ that were estimated as a proportion of the 5th-year adult population due to the lack of postfire skeletons;

[c] s = shrub, ss = subshrub, su = suffrutescent, woody at base, li = liana;

[d] This species has the capacity to resprout but failed to survive fire and thus functions as an obligate seeder.

many species, seedling establishment occurs largely as a single pulse in the first growing season after fire. These include *obligate seeding* species that are entirely dependent on this seedling pulse for persistence and *facultative seeding* species that also resprout. However, not all resprouting species have dormant seed banks. In some species, seedling recruitment is dependent on the flowering of resprouts in the first year that produce a transient seed bank, which germinates *en masse* in the second postfire year. Other species produce multiple pulses of seedlings during early succession, as well as exploiting gaps in mature shrublands (e.g. DeSimone & Zedler, 1999). Possible explanations for these different patterns are that the different timing of seedling populations in the sage scrub community is due to selection to avoid competitive interactions, environmental filtering effects, or to phylogenetic constraints.

The sage scrub sites shown in Table 12.1 had a total of 21 woody species in common and there was evidence that these communities were structured due to interactions such as competition. This is indicated by the highly significant co-occurrence pattern. Using EcoSim null model tests (Gotelli & Entsminger, 2006), there was less co-occurrence of all possible pairs of species than predicted if species were distributed randomly ($P < 0.001$). One means of investigating the extent to which resource competition might structure seedling communities is with a trait-based approach that considers seedling recruitment patterns as guilds or functional types, for example, those with a first-year pulse of seedlings, those with second-year pulse, and those with multiyear recruitment (Table 12.1). Species in the same guild might be expected to be similar in their resource use and to compete more with each other than with species from other guilds. EcoSim tests whether the co-occurrence index among these guilds differs from that expected by chance alone. In this analysis, there was a probability of $P = 0.09$ that co-occurrence of guilds is entirely by chance, suggesting only a slight tendency toward structuring of these communities based on combinations of seedling recruitment modes.

However, null models assume all taxa assort at random and this assumption may not hold if there were significant environmental filters at work. In this sage scrub community, there are environmental factors tied to recruitment guilds (Table 12.2). Species with dormant seed banks that recruit largely in the first-year after fire comprise a larger proportion of the community on hot interior sites with sandy soils and low phosphorous content, whereas the multiyear recruiting guild preferred the opposite conditions. In addition, fire severity provides an additional filter by favoring the first-year recruiting guild. These analyses were made at the site level, but it is likely that within site microhabitat differences for some of these factors might also be a force in structuring seedling communities.

In light of the strong effect of distance from the coast on climate, these data were grouped by region (coastal vs. interior) rather than by guild and in this analysis with EcoSim there was a significant ($P < 0.001$) departure from randomness, indicating that co-occurrence

Table 12.2 Regression analysis, relating the proportion (total 5-yr seedling density) for each seedling guild to environmental factors, for the communities in Table 12.1, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n = 48 sites.

	r				
	Coast	Insolation	Sand	Soil P	Fire Severity
First-year pulse	+ 0.44 **	+ 0.31 *	+ 0.48 ***	− 0.35 *	+ 0.38 **
Second-year pulse	− 0.51 ***	ns	+ 0.32 *	ns	ns
Multi-year recruit	ns	− 0.36 *	− 0.46 ***	+ 0.42 **	− 0.38 **

structure was significantly different in the two regions. Analyzing these regions separately revealed that at least for the interior sites, there was a significant ($P = 0.018$) chance that the combinations of different recruitment patterns across sites was not the result of the random distribution of taxa, rather there were consistent ratios. It would appear that these seedling communities are the result of both environmental filters that control different seedling recruitment guilds as well as interactions between different guilds that select for particular combinations of guilds.

12.5 Conclusions

Seedling communities are structured by multiple factors that vary with the vegetation type and landscape position. Here we have focused on woody plant seedlings because the life stages are more distinct than in fast-growing herbaceous species. However, it seems likely that much of this discussion is applicable to herbaceous life-forms as well. The relative contribution of seedling dynamics to later community structure and function can be substantial. In some communities, this regeneration niche seems to be the primary focus of selection whereas in other communities selection is most intense on the adult stage. Seedling community structure may be driven by selection to avoid competitive interactions, environmental filtering effects, or phylogenetic constraints and sorting out the relevant strengths of each of these is a challenge. Testing these ideas across a range of community types will help forge a new perspective on the ecology of seedling communities.