Conifer Regeneration after Forest Fire in the Klamath-Siskiyous: How Much, How Soon?

J.P.A. Shatford, D.E. Hibbs, and K.J. Puettmann

ABSTRACT

The increasing frequency and extent of forest fires in the western United States has raised concerns over postfire management actions on publicly owned forests. Information on ecosystem recovery after disturbance is lacking and has led to heated debate and speculation regarding the return of forest vegetation after disturbance and the need for management actions. One critical question emerges, will these ecosystems recover on their own, and if so, over what time frame? We report on one aspect of recovery, the spatial and temporal variation of natural conifer regeneration evident 9–19 years after forest fires in California and Oregon. In contrast to expectations, generally, we found natural conifer regeneration abundant across a variety of settings. Management plans can benefit greatly from using natural conifer regeneration but managers must face the challenge of long regeneration periods and be able to accommodate high levels of variation across the landscape of a fire.

Keywords: natural regeneration, fire ecology, early succession

The rugged mountains of northern California and southwest Oregon, also known as the Klamath-Siskiyous ecoregion, support productive forest, are unusually diverse biologically, geologically, and topographically and have a history of frequent wildfire of low and mixed severity (Whittaker 1960, Agee 1993). Between 1970 and 2004, more than 600 wildfires burned over 2 million ha in Oregon and over 6 million ha in California. In 2002, the Biscuit Fire alone encompassed some 200,000 ha of mixed conifer forests of the Rogue/Siskiyou National Forest and was the largest fire in Oregon's recorded history. The US Forest Service has since become embroiled in a controversy over salvage logging and forest recovery (Nazzaro et al. 2006). As key components of ecosystem recovery, the regrowth of trees and other vegetation after disturbance is a focal point in this controversy.

Fire has long played a role in shaping plant communities across the Klamath-Siskiyous ecoregion (Agee 1993, Taylor and Skinner 1998). Plentiful winter rains followed by summer drought and lightning storms set conditions for dry fuels, ignition, and fire spread. Extensive evidence indicates that forest fires and natural regeneration have been recurring events, following in repeated fashion decade after decade across a wide range of forest types (Atzet et al. 1992, Agee 1993, Sensenig 2002). The presence of forests blanketing the mountainous landscape attests to the ability of the vegetation and its individual species to survive or regenerate after fire. An agent of destruction, but also an agent of renewal, fire plays a dominant role in the forests of the Klamath-Siskiyous region, making them, practically speaking, "born of fire."

Considerable evidence from fire scars, tree ages, and tree growth patterns suggests that frequent low and moderate severity fires have been common in the Klamath-Siskiyous (Agee 1993, Taylor and Skinner 1998), resulting in low-density, multiaged stands (Sensenig 2002). Fire suppression efforts during the 20th century have altered the fire

regime and have led to changes in forest structural characteristics (Agee 1993, Sensenig 2002). High-severity, stand-replacing fires also have been known in this region, where complex topography and fire behavior typically resulted in a patchy distribution of canopy openings, intact stands, and scattered surviving trees (Wills and Stuart 1994, Alexander et al. 2006).

The prognosis of forest recovery after high-severity forest fire is uncertain. A history of regeneration failures after fires and logging raised concerns over the long-term sustainability of conifer forests in the region (Hobbs et al. 1992). Large brushfields dominated extensive areas in southwest Oregon in the mid-20th century and may have resulted from fires set by early settlers, ranchers, and miners (Hayes 1959). Limited conifer regeneration over long periods (10–50 years) fostered concerns that such areas would remain unforested indefinitely (Gratkowski 1961). Additional regeneration failures occurred after clearcut harvesting, and attempts to improve the regeneration environment through shelterwood cutting had mixed results (Stein 1986). Given this history of uncertainty, questions arose as to whether conifers would regenerate after the high-severity forest fires of recent times. Fears emerged that the brushfields common to the Klamath-Siskiyous highland in the early 1900s (Hayes 1959, Gratowski 1961) would become a dominate feature of the forests of the 21st century as well (Sessions et al. 2004).

Of particular concern was the competitive advantage of broad-leaved shrubs and hardwoods that may result after the removal of the conifer overstory by fire. Hardwoods, particularly tanoak (*Lithocarpus densiflora*), madrone (*Arbutus menziesii*), and oaks (*Quercus* spp.), resprout vigorously after fire (Brown and Smith 2000). The rapid growth of seed-bank species such as *Ceanothus* and their association with nitrogen-fixing bacteria can lead to extensive shrub cover in early successional communities in the region (Hanson and Stuart 2005). Without active reforestation, conifers may have little or no window for regeneration amid the rapidly growing shrubs and hardwoods (Hobbs et al. 1992, Sessions et al. 2004). Along with competition for moisture and growing space, high levels of seed predation and high surface soil temperatures result in high mortality rates within the 1st year (Minore and Laacke [1992] and references therein). Extensive research has documented the advantage of planting conifers and controlling shrubs to increase tree density and growth over the early years of stand development (Hobbs et al. 1992, Zhang et al. 2006).

Today, many postfire action plans regard treeplanting and vegetation control as a relatively straightforward and effective solution to the problem of forest renewal (Lindenmayer 2006). Little is known about how burned areas will recover on their own, how they might differ from stands managed after fire, or how these differences relate to the rate of forest recovery after fire over the short term (1–2 years) or longer (1–2 decades) time frames. The lack of information concerning ecosystem recovery, specifically natural conifer regeneration after wildfires, has allowed speculation on complex ecological processes. For example, in a recent 2-year study of conifer survival with and without salvage logging in southwest Oregon, Donato et al. (2006) concluded that postfire management activities 2 years after a fire killed most natural tree regeneration and may be counterproductive to forest recovery. This conclusion contradicted recommendations of a recent policy analysis for southwest Oregon, which argued that burned areas can develop into unproductive shrub fields that persist for "decades, perhaps centuries" and that postfire salvage logging and treeplanting would speed the recovery of complex conifer forests and provide revenue from timber extraction (Sessions et al. 2004).

We report here on the abundance of natural regenerating conifers occupying sites 9–19 years after stand-replacing wildfires in northern California and southwest Oregon. Our findings redefine concepts of the role and reliability of natural regeneration in high fire frequency systems in the context of ecosystem management (Christensen et al. 1996). Additionally, they highlight the role of temporal and spatial variation as an inherent feature of forest development. Forest managers relying on natural regeneration should feel increased confidence and need to develop plans that can accommodate high levels of variation and accept the prolonged time line of the regeneration process.

Methods

We conducted a stratified random sampling of natural regeneration at locations that burned at high severity within fires that
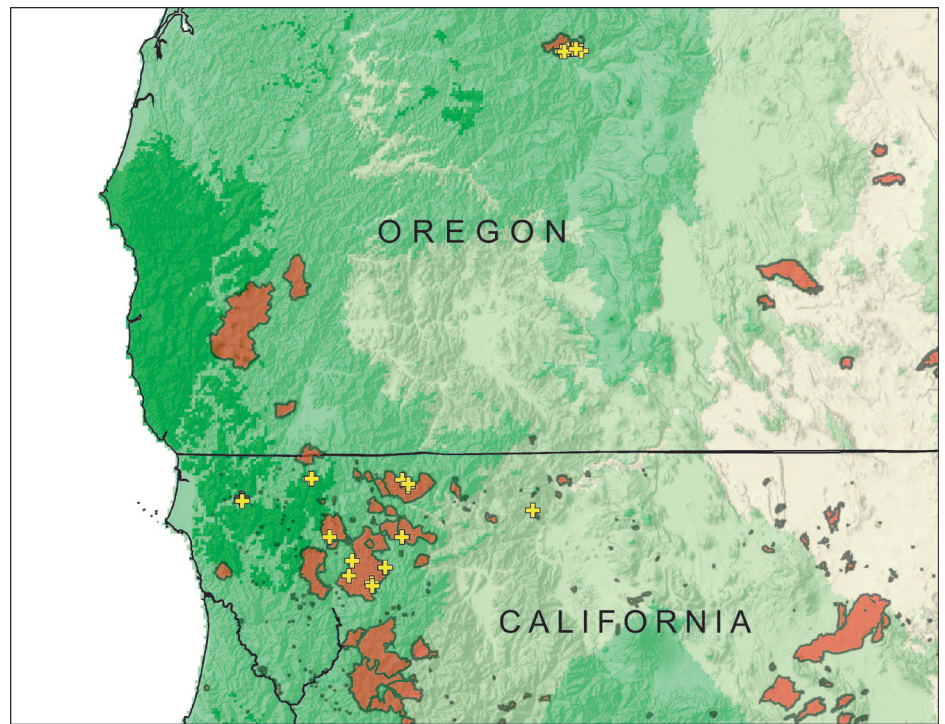

Figure 1. Variation in climate and topography contribute to the diversity of forest types across northern California and southern Oregon. Annual precipitation across the region ranges from less than 50 cm/year (yellow) to more than 200 cm/year (dark green). Red polygons indicate wildfires dating back to 1970. Study sites (yellow crosses) were located within forest openings that resulted from forest fires between 1987 and 1996. The study included parts of the Umpqua National Forest, Oregon, and the Klamath and Six Rivers National Forests, California.

burned 9–19 years earlier in southern Oregon and northern California. A Mediterranean climate predominates in the area: hot, dry summers and cool, moist winters. Annual rainfall ranges considerably across the district from 50 cm/year (Yreka, California) to 237 cm/year (Gasquet, California). Across the same area, January mean temperatures range from 1 to 2° C and July mean temperatures range from 20 to 22° C. Elevation ranges from 200 to 500 m above sea level (asl) within inland valleys and over 2000 m on ridgetops and peaks.

Data were collected to assess natural regeneration across a range of sites stratified by elevation, aspect, and distance from seed source. All field sampling took place in 2005 in eight areas burned between 1987 and 1996 (Figure 1). The fire areas ranged from 350 to 28,000 ha (mean, 8,134 ha). Thirty-five plots were established across a broad gradient of productivity and forest types. Our sampling encompassed three broad forest types (hereafter plant series) ranging from dry to wet (Atzet et al. 1992). Within the Douglas-fir series, sites ranged from dry, low-elevation interior valleys occupied by the Douglas-fir/ponderosa pine series to more mesic, transitional, and inland sites within the Douglas-fir/tanoak series (Atzet et al. 1992). In the drier Douglas-fir sites, oceanspray (*Holodiscus discolor*), trailing snowberry (*Symphoricarpos hesperius*), and deer brush (*Ceanothus intergerrimus*) were common and abundant (4–40% cover). On Douglas-fir/tanoak sites, red huckleberry (*Vaccinium parvifolium*) and hairy manzanita (*Arctostaphylos columbiana*) were common. At higher elevations, we encountered the cooler and more mesic white fir series (Atzet et al. 1992). White fir understory associates included snowbrush (*Ceanothus velutinus*) and manzanita (*Arctostaphylus* various species).

Candidate sites were identified from geographic information system (GIS) data on fire occurrence and management history in the Klamath, Rogue/Siskiyou, and Umpqua National Forests. Sample sites met three general criteria: (1) canopy-replacing wildfire, 9–19 years earlier, (2) more than 90% tree mortality due to fire, and (3) no postfire salvage logging or treeplanting. For all sites, we obtained and evaluated aerial photographs taken 1–3 years after fire. From these we identified openings from high-severity fires that were previously conifer dominated (snags present). Plot locations were assigned

Figure 2. A young stand of mixed conifer, Douglas-fir (*P. menziesii*), pine *Pinus* (various), and incense cedar (*C. decurrens*) seedlings and saplings regenerated after a high-severity wildfire in 1987 burned this area within the Douglas-fir plant series above Grider Creek, California. (Photo: J. Shatford, UTM 10 481034E 4619894N.)

Figure 3. Eighteen years after a high severity wildfire in the Klamath highlands of northern CA, the density of white fir (*Abies concolor*) seedlings ranged from 1,200 to 16,000/ ha. Tree ages indicated that seedling establishment may be limited for several years after fire followed by multiple years of abundant seedling establishment. (Photo: J. Shatford, UTM 10 470403E 4602356N).

randomly using a combination of photo overlays and random number allocations. All plots were located 50–400 m from a seed source (a stand of mature conifers) to explore distance effects. We avoided areas with serpentine substrate but did not adjust plot

locations to avoid rock outcrops, poison oak, or dense brush.

A 0.048-ha sampling plot was comprised of 30 4 × 4-m (0.0016 ha) cells in a grid of 3 × 10 cells/plot. Each cell, roughly equivalent to 1/600 ha (1/250 ac), provided a means to assess the dispersal of regenerating dominant (defined later) conifers. A plot with at least one conifer in each cell was considered fully stocked. The percent cover and median height for each shrub and hardwood species were estimated visually in each third of the plot (12 × 12 m) and then averaged for the entire plot.

For each plot, we tallied conifer seedlings by species. Per-hectare conifer regeneration density was estimated from sample plots stratified by plant series. We aged the largest (dominant) seedling in each cell both by counting branch whorls and by cutting or coring at the base and counting annual growth rings (Sheppard et al. 1988). For dominant regeneration, we calculated (1) year of establishment, (2) live crown ratio, and (3) growth rate (seedling height divided by total age). We used the age of the oldest seedling in each cell to determine when the cell was first successfully occupied. For each year after the fire we calculated the proportion of cells occupied by at least one seedling. Graphical comparisons of stocking rates were stratified by plant series and decade since fire (to avoid confounding fires from roughly 10 years ago with those ~20 years ago). Total tree density estimates were stratified only by plant series. We averaged the number of dominant conifers originating in a given year by time since fire and plant series. The average rate of establishment (dominant seedlings only) was plotted for each year after the fire until the year of the survey. The hardwood and shrub cover (percent) and growth rate of the dominant cohort was calculated as the average for each plot (n = 35).

Results and Discussion

Patterns of Seedling Establishment. In 2005, we determined the spatial and temporal variation of conifer establishment after eight wildfires that occurred between 1987 and 1996 throughout the Klamath-Siskiyous region. Generally, conifer regeneration on our study sites was abundant and the period of establishment was surprisingly protracted (extended) and variable.

Conifer density varied by plant series. Total conifer density ranged over three or-
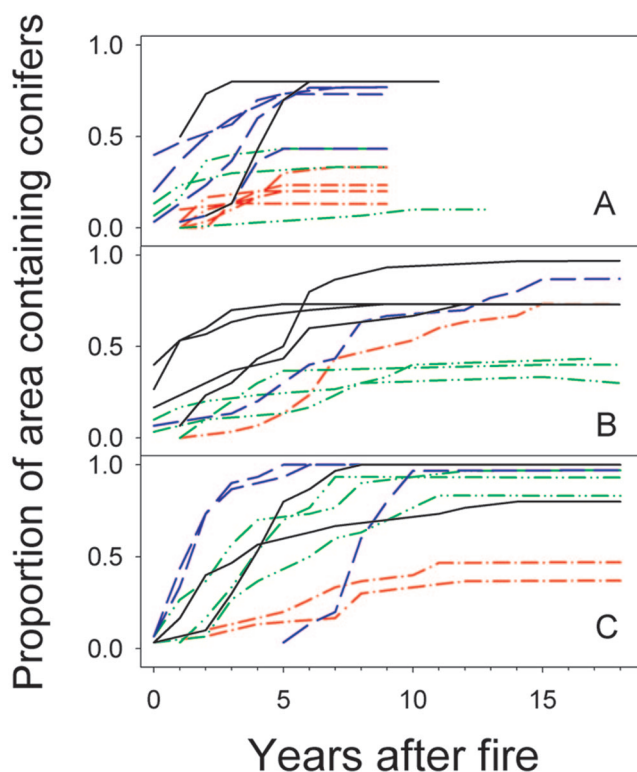

Figure 4. Changes in conifer stocking over time since wildfire (stocking = proportion of 1/600 ha cells in each plot containing one or more established conifers). The lack of similarity among shape of curves or peaks in years after fire suggests the importance of local controls, i.e., plot level variation. (A) Establishment after fires of 1992–1996 on low-elevation sites; (B) establishment after fires of 1987 on low-elevation sites (Douglas-fir and Douglas-fir/tanoak series); (C) establishment after fires of 1987 on high-elevation sites (white fir series) in the Klamath-Siskiyous region. Red (single dotted), green (double dotted), blue (long dash), and black (solid) lines indicate quartiles of increasing total seedling density (as opposed to stocking) observed at the time of our survey. Because of variation in spatial distribution of seedlings within a plot, a high seedling density did not always result in a high proportion of area occupied.

ders of magnitude, averaging 1,694 trees/ha (tph; 83– 8,188 tph; n = 24) in the lower elevation Douglas-fir and Douglas-fir/tanoak series combined and 7,621 tph (688–16,771 tph; n = 11) in the higher elevation white fir series. Within the Douglas-fir series, an average of 51% (±7.8 SE, n = 24) of the seedlings were Douglas-fir (*Pseudotsuga menziesii*), 14% (±4.0 SE) were ponderosa pine (*Pinus ponderosa*), 17% (±6.7 SE) were knobcone pine (*Pinus attenuate*), and 8% (±3.5 SE) were incense cedar (*Calocedrus decurrens*), with the remainder (~10%) consisting of sugar pine (*Pinus lambertiana*), western white pine (*Pinus monticola*), and white fir (*Abies concolor*; Figure 2). Among the white fir series, seedling counts averaged 80.3% (±8.2 SE; n = 11) true firs (*A. concolor* and *Abies magnifica*) and 18.4% (±7.9) Douglas-fir with lesser amounts of knobcone pine, incense cedar, sugar pine, and western white pine (Figure 3). The den-

sity of conifers was equal to or greater than typical densities in 60- to 100-year-old stands in this region (250–2,500 tph; Sensenig [2002]). Survival and growth of only a portion of seedlings would suffice to develop forested conditions. Old-growth forests in the region, dominated by trees 250 years or older, commonly contain 50–100 tph (Sensenig 2002).

On all sites conifer density increased over our study period. The establishment of up to 30 well-distributed dominant seedlings per plot was seldom synchronized within an individual plot, fire, or across the landscape in a given year (Figure 4). For example, the time required for seedlings to occupy the 30 cells in a 12 × 40-m plot exhibited the full spectrum of possibilities: immediate and rapid filling, initially delayed (4–9 years) and then rapid filling, slow but constant filling, and chronically limited (Figure 4).

When averaged across sites, this diversity of patterns is reflected in a yearly accumulation of seedlings after fires, with an eventual and gradual decline of establishment rate (Figure 5). Surprisingly, up to 19 years after a fire, some new and locally dominant regeneration still was appearing. We observed local incidents of seedling pulses (e.g., within a given plot), but there was no broadscale synchronization of seedling recruitment for any given year (Figure 4). Thus, although there were undoubtedly some good seed years during the period of observation (19 years), they did not result in pulses of established regeneration (Means 1982).

Conifers are dependent on regeneration from seed that likely comes from nearby sources. Both conventional wisdom and seed dispersal graphs suggest that the majority of seed fall occurs near the seed source with seed rain trailing off to very low seed densities by 200 m from a seed source, although exact dispersal patterns vary with species, wind patterns, topography, and other factors (Isaac 1940, Minore and Laacke 1992, Greene and Johnson 1996). We observed as many as 84–1,100 tph greater than 300 m from a seed source (Figure 6), suggesting that at this scale, forest recovery is not a simple function of distance to surviving trees that act as seed sources (Nathan and Muller-Landau 2000). There was no significant effect of distance from seed source on tree density for either the Douglas-fir series ($F = 0.66$; $P > 0.42$; $n = 24$) or the white fir series ($F = 1.89$; $P > 0.20$; $n = 11$). Our seed sources often were dense patches of trees providing abundant seed, thus increasing the probability of seed traveling long distances (more than 350 m). These observations suggest that the mechanism(s) behind long-distance seed dispersal are not entirely clear and that models for long-distance seed dispersal of conifers are incomplete.

Roles of Shrubs and Hardwoods. A major component of ecosystem recovery consisted of shrubs and resprouting hardwood trees (25–95% aerial cover; 47 species). Across the range of Douglas-fir forest types (from the drier Douglas-fir through Douglas-fir/tanoak series), abundance of conifers was positively associated with cover of hardwoods and shrubs (Figure 7). Because this range of Douglas-fir associations describes a continuum of increasing productivity (Atzet et al. 1992), we interpret the positive relationship between hardwood and
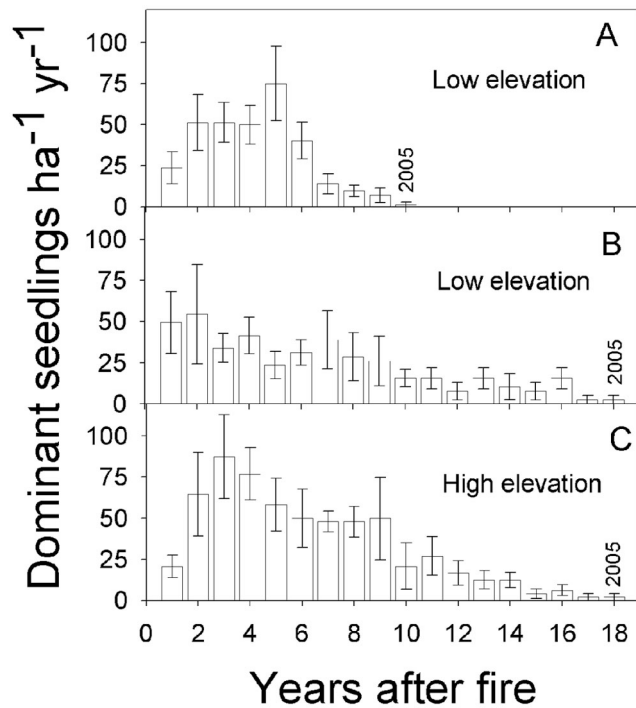

Figure 5. Dominant conifer abundance by year of establishment. (A) Establishment after fires of 1992–1996 on low-elevation sites; (B) establishment after fires of 1987 on low-elevation sites (Douglas-fir and Douglas-fir/tanoak series); (C) establishment after fires of 1987 on high-elevation sites (white fir series) in the Klamath-Siskiyous region. Error bars indicate ± SE.
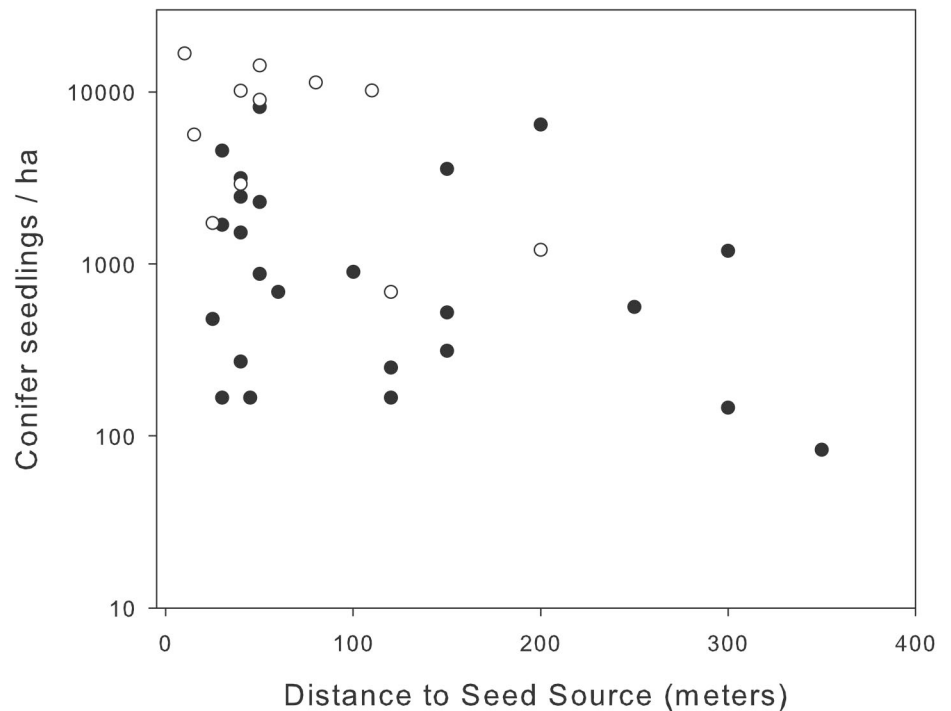

Figure 6. Tree density (tph) in relation to distance to seed source (m) for two plant associations, Douglas-fir and Douglas-fir/tanoak series (closed circles) and white fir series (open circles).

shrub cover and seedling abundance as a response to increased site productivity and availability of resources to vegetation in general (Whittaker 1960). In contrast, across sites within the white fir series, the opposite trend was observed as conifer seedling abun-

dance decreased with hardwood/shrub cover (Figure 7). Seedling establishment was, however, conspicuously high on all sites within the white fir series; hence, competition from broad-leaved species does not seem to present a serious obstacle to conifer establishment there.

We found that conifer seedlings were frequently overtopped by shrubs and hardwoods (Figure 8). Average height of the most common shrub species, deerbrush, snowbrush, and greenleaf manzanita (*Arctostaphylos patula*), were 1.9, 1.2, and 1.1 m, respectively. However, there was no evidence of recent conifer mortality or suppression leading to death. Dominant conifers had live crown ratios averaging 68% (*n* = 35) and moderate height growth (10.2 cm year 1 over the last decade; ±4.9 SD; range, 2.7–22.5 cm year 1; *n* = 35). Over one-third of the conifers were greater than 1.5 m in height with an average height for Douglas-fir of 1.2 m (±0.23 SE). It is quite likely that height growth of shrubs has slowed after 9–19 years (Brown and Smith 2000) while tree height growth continues to slowly increase. We predict that conifer mortality will remain low and height growth will accelerate as individuals continue to emerge above the shrub layer (Conard and Radosevich 1982).

As the rate of forest development differs among naturally regenerating and planted areas, managers must decide what is most appropriate for a given site. Several tradeoffs warrant consideration. The density of naturally regenerating conifers appears adequate to provide stocking across the forest types we investigated (but see Hayes [1959] and Stein [1986]). Although the density of conifer regeneration was not completely restricted by the presence of broad-leaved species, in most places their growth rate most certainly has been (Hobbs et al. 1992, Tesch et al. 1993). A reduction in terms of timber production can be expected in the short term (Hobbs et al. 1992), but over the long run the results may be less certain (Busse et al. 1996, Zhang et al. 2006). Although short-term gains may be made from shrub removal, long-term benefits of increased nutrient levels and ultimately sustained conifer growth warrants additional consideration (Busse et al. 1996). The appearance of broad-leaved species from stumps, roots, or seeds can stabilize soils and reduce erosion hazards after fires. Where heat or drought may be limiting seedling establishment, shrubs facilitate nat-
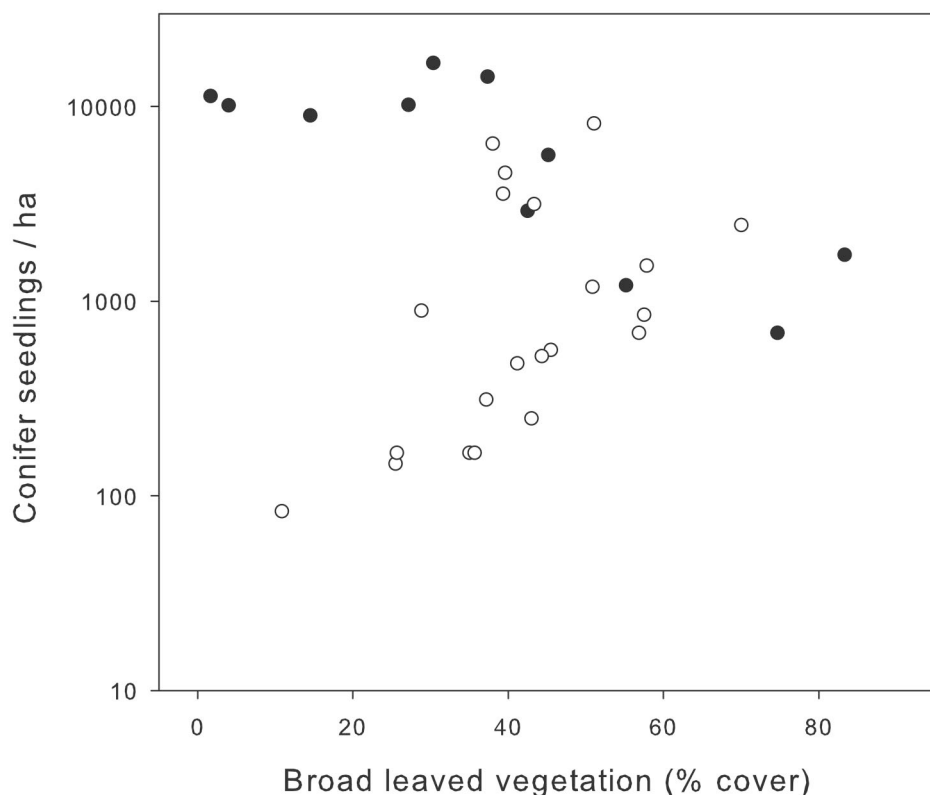

Figure 7. Relationships between conifer seedling density and percent cover of broad-leaved perennials (hardwoods and shrubs) among plant associations, Douglas-fir and Douglas-fir/tanoak series (closed circles), and white fir series (open circles).

ural tree regeneration and growth by providing shade and conserving moisture (Minore 1986, Kitzberger et al. 2000). The presence of vegetation also may play a critical role in attracting birds and mammals that act as agents of seed dispersal (Vander Wall 1990). Areas of shrub and hardwood cover benefit a variety of wildlife species (Alldredge et al. 2001).

Conclusions

Our study advances an understanding of natural forest development after wildfire in the diverse Klamath-Siskiyous region (Minore and Laacke 1992). Clearly, natural regeneration of conifers is an intrinsic response to fires in most locations (Turner et al. 2003), and forests are recovering across the entire range of forest types we investigated and at considerable distances from seed sources.

The establishment of conifers after wildfire was highly variable from year to year, and place to place, resulting in high variation in tree density and size. Understanding factors associated with this variation warrants additional attention. Given the role of aspect, elevation, and climate on vegetation across this region (Atzet et al.

1992), evaluating their combined influence may provide further insights.

Forest managers who use natural regeneration will need to develop planning and decision tools that can accommodate spatial variability and include thresholds for regeneration success with a much longer regeneration phase than commonly accepted in the region (Minore and Laacke 1992). In contrast with previous observations (Hayes 1959, Stein 1986), our findings suggest that the prognosis for achieving reasonable conifer densities are fair to excellent, even on sites with high cover of broad-leaved shrubs and hardwoods. Although conifer growth may be delayed by competition over the short term, benefits in terms of wildlife habitat and site fertility should be considered.

Viewing ecosystem recovery as a variable and dynamic process highlights the limitations of short-term studies (Donato et al. 2006) that provide an incomplete picture of the regeneration process. In addition, assertions that burned areas, left unmanaged, will remain unproductive for some indefinite period (Sessions et al. 2004) seem unwarranted. A more complete understanding of the tradeoffs among management options is

Figure 8. A naturally regenerated Douglas-fir (*P. menziesii*) seedling emerges above a sea of snowbrush (*C. velutinus*) 10 years after a high-severity wildfire. The large number of conifer seedlings not visible here among the shrub cover provided an estimate of 917 seedlings/ha for this site in the western Klamath National Forest. (Photo: J. Shatford, UTM 10 453011E 4609716N.)

necessary to resolve current controversies. To date, few studies evaluate outcomes of different management approaches across a diverse set of conditions and over extended time frames. Past research has shown that salvage logging after wildfire in the Klamath-Siskiyous can influence the abundance of trees, shrubs, and herbaceous cover, even years later (Hanson and Stuart 2005). In other parts of the region, natural regeneration after logging or other disturbance may match or exceed that achieved by reforestation efforts (Bock et al. 1978, Miller et al.

1993), or it may lag behind. However, even with information from 20 years of forest dynamics, successional development can not be precisely predicted for specific locations. This highlights the challenge to integrate a wide range of forest conditions across a landscape to meet the diverse set of goals and needs imposed by society (Christensen et al. 1996, Nabuurs et al. 2001).

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