

# **11** *Natural Regeneration*

*Don Minore*

*Robert J. Laacke*

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## INTRODUCTION

Natural regeneration is the renewal of a tree crop by self-sown seed or by vegetative means (Ford-Robertson 1971). Foresters in southwestern Oregon and northern California relied on it heavily until the early 1950s (Dunning 1923, Zaerr et al. 1981). As economic considerations and the pressures of intensive management began to increase, forest managers shifted to artificial means of regeneration. Direct seeding was tried for a short time, but it was quickly dropped in favor of planting nursery-grown seedlings combined with controlling vegetation after planting. As a result, natural regeneration has not played a major role in management plans for the last 30 years. Nevertheless, a significant portion of the clear-cut plantations in California owe their successful establishment and their species diversity to unplanned natural regeneration, which accounts for much of their stocking even after multiple replantings (data on file at Pacific Southwest Forest and Range Experiment Station, Redding, California).

Dramatic cost increases in all aspects of artificial regeneration have raised the per-acre investment to extraordinary levels. That high cost makes it increasingly difficult to answer critics who challenge the "clear-cut-and-plant" concept on a variety of biological, ecological, and aesthetic grounds. Society is demanding major changes in the management of forest land, and those changes are beginning to be institutionalized in law and policy. They include a shift in emphasis away from management techniques and regeneration strategies that rely solely on artificial regeneration.

The authors of this chapter predict that natural regeneration will become a consideration in most management plans during the next decade, either alone or as a supplement to the more direct artificial methods. Because natural regeneration has been out of favor for so long, there is little in the way of recent experience to rely on in the field, and there is no comprehensive body of research available for the region addressed in this book. Therefore, pertinent information from other areas has been included with the material developed in southwestern Oregon and northern California. The natural regeneration of conifers is discussed here; regeneration of hardwood species is treated in Chapters 7 and 16.

## ADVANTAGES AND DISADVANTAGES OF NATURAL REGENERATION

### *Advantages*

Natural regeneration tends to be considerably cheaper than artificial regeneration (Vesikallio 1981, Petersen and Mohr 1984, Horton 1985). Early in the rotation, this difference can amount to a significant economic advantage.

The biological differences between planted and naturally regenerated seedlings can influence both early and late growth. Transplanting shock is avoided in naturally established seedlings, and root distribution is better than it is in planted seedlings. Furthermore, naturally

established seedlings have much longer roots in proportion to shoots than nursery seedlings of the same species, with shoot-to-root ratios in natural seedlings of about 1:4 or less and those in nursery stock of about 1:1 to 2:1 or more. The nursery stock has more top and a proportionately smaller, more loosely anchored root (Stein 1978). Roots of planted seedlings also tend to be more kinked, spiraled, and twisted than those of natural seedlings (Preisig et al. 1979, Carlson et al. 1980, Auberlinder 1983). These abnormalities can persist for 10 years after outplanting (Nichols and Alm 1983).

Natural selection has matched trees to their sites for millennia. For example, Douglas-fir seedlings produced from seeds gathered on south slopes have more drought resistance than those produced from nearby north-slope seeds (Ferrell and Woodard 1966). The differences between Douglas-fir genotypes are related to local variations in environment (Hermann and Lavender 1968, Campbell 1979, Silen and Mandel 1983, Sorensen 1983). Indeed, it seems that every slope and ridgetop has its own select population of conifers. Naturally regenerated stands may serve as genetic reserves (Neale 1985), and their progeny may be even better than artificially bred "improved" stock in many places because every site does not have representative parent stock in the tree improvement program.

Nursery seedlings are best planted early in the spring, when access to upper-elevation sites is often prevented by snowpack and poor road conditions. Natural regeneration avoids this problem as well as several others, including the difficulties of selecting suitable planting spots and digging holes in rocky soils.

Public dissatisfaction with large clearcuts is creating a trend toward smaller harvest units and the retention of some tree cover. Because these practices make artificial regeneration more difficult and less profitable, natural regeneration becomes a more feasible alternative. On many sites, regeneration can be achieved before the harvest cut by utilizing naturally established seedlings, and advance regeneration may be the most reliable source for new stands at high elevations in mountain hemlock associations (Chapter 5). Advance regeneration can also be promoted by silvicultural means. If the harvest can be managed so as to save enough

high-quality seedlings on sites where advance regeneration is present, the expense and risk of planting (as well as the unappealing sight of bare ground) can be avoided. In addition, successful use of advance regeneration can shorten the rotation (Sandvic 1986).

The poorer the site, the less the economic justification for planting (McClay 1955, Tedder 1982). Natural regeneration is frequently used on sites where growth rates do not warrant the large investment required for planting. Natural regeneration is also feasible on high-quality sites where harvest scheduling can mitigate potential delays caused by the vagaries of climate and the year-to-year fluctuations in seed availability.

### *Disadvantages*

Failures of natural regeneration are common in clearcuts on hot, dry south slopes, on sites where frost is a hazard, and on sites where seed sources are inadequate (Hermann 1978). Successful natural regeneration requires mitigation of these conditions when they exist, usually by leaving tree cover. Tree cover does not guarantee survival; planted stock survived better than natural seedlings under a southwestern Oregon shelterwood when survival was measured on a tree-by-tree basis (Helgerson et al. 1982), but tender germinants require more overstory protection than robust, 2-year-old planting stock. Where that overstory cannot be provided and clear-cutting is dictated by stand conditions or other considerations, artificial regeneration is the only means available. When natural regeneration fails and a site must be planted, the delay is expensive (Horton 1985), though no more costly than replanting a failed artificial regeneration effort.

The regeneration methods best suited to natural regeneration are often less economical than clear-cutting (Streeby 1977). When seed tree, shelterwood, or selection methods are practiced, the repeated entries compact the soil and damage regeneration and residual trees. Control of competing vegetation can be more difficult under an overstory. It takes extra time, care, and money to manage an overstory removal cut that produces a forest with an optimal combination of desired products and values. It also takes understory seedlings of sufficient quality and quantity to survive the

removal of the overstory (Laacke and Fiddler 1986). In short, the whole process—from site planning and administration through slash disposal—is more difficult where mature trees and regeneration must be protected.

The creation of appropriate seedbeds for natural regeneration may require machinery and techniques not usually used in artificial regeneration, including underburning (Petersen and Mohr 1984), cultivation (Musser 1985), and tractor scarification. Prepared seedbeds deteriorate over time; if the preparation is not in sequence with a seed crop, the investment in preparation could be wasted (Oliver et al. 1983).

Good seed crops are infrequent and irregular for most species, and they vary with location as well as with the nature and timing of stand manipulation. The pines provide at least a year's warning when a seed crop is going to occur, but other species take less than 2 years to produce mature seeds. For these species, the lead time for planning the harvest and the seedbed preparation is limited to several months. Even when cone counts indicate that a useful crop is being produced, rodents and birds often destroy most of the seeds (Gashwiler 1967 and 1970). Under these uncertain conditions, it is difficult to plan and coordinate operations that involve people and machinery.

Prompt planting can provide a 1- or 2-year lead over immediate post-harvest natural regeneration (Shearer 1982), and successful natural regeneration is not always immediate. Five to 15 years may be required to obtain full stocking in subalpine environments (Minore and Dubrasich 1981). Similar delays are not uncommon at lower elevations. Whether such a delay is more costly than a failed artificial regeneration attempt depends on how many times the plantation must be planted and how the capitalized planting costs affect the economics of the stand by the time it is harvested. In either case, failure to comply with provisions of the Oregon and California forest practices laws (summarized in Chapter 8) creates legal as well as economic problems. Whenever full stocking is obtained, natural regeneration is frequently overabundant in places and must be thinned later.

When natural regeneration is used, the species to be managed are limited to those growing on or adjacent to the site. Shade-tolerant species tend to predominate in a new stand on a site where

overstory protection is required for relatively long periods. Sometimes the presence of a host-specific pathogen or parasite may make a species change desirable; although dwarf-mistletoe infection can be avoided in the true firs by removing overhead infection sources before the natural regeneration is 1 m tall (Scharpf 1969 and 1978), some diseases are not so amenable to silvicultural control. Natural regeneration would thus not meet management objectives on such a site.

Artificial and natural regeneration require essentially the same conditions following establishment. Both grow best free from an overstory and both suffer from vegetative competition; thus, release is commonly necessary. The initial size advantage enjoyed by planting stock is sometimes maintained and increased in the field if the initial shoot-to-root ratios are sufficient for rapid early growth (Smith et al. 1968).

Perhaps the clearest disadvantage of natural regeneration is its inability to benefit from genetic improvement programs that increase survival and growth. A commitment to natural regeneration is a commitment to forgo the benefits of planting genetically improved stock (Streeby 1977).

## SEED SUPPLY

### *Production*

Some seeds are produced nearly every year on nearly every site, but the timing of large seed crops is variable (Table 11-1). Periods range from 1 year for lodgepole pine seed to intervals of 2-11 years between large crops of Douglas-fir seed. Although cause-and-effect relationships have not been determined, weather patterns have been correlated with seed production for some species. An abundant Douglas-fir seed crop tends to be preceded by a cool summer 2 years before seedfall, followed by a cold, clear winter, a wet spring, and a final warm January (Lowry 1966, Eis 1973). A similar combination of climatic factors probably influences seed production in grand fir (Eis et al. 1965). Ponderosa pine seed production seems to be best when summer temperatures are above average for the year when strobilus initials are formed (Daubenmire 1960). Douglas-fir cone crops tend to be larger on poor sites than on good sites (Isaac

Table 11-1. Minimum seed-bearing ages and intervals between large seed crops for major conifer species. From Franklin (1974), Harris (1974), Krugman and Jenkinson (1974), Owston and Stein (1974), Ruth (1974), Schopmeyer (1974), Stein (1974)

Species	Minimum seed-bearing age	Intervals between large seed crops
	Years	
Douglas-fir	10	2-11
Grand fir	20	2-3
White fir	40	2-4
Red fir	35-40	2-3
Shasta red fir	30-40	2-3
Ponderosa pine	16-20	2-5
Jeffrey pine	8	2-4
Sugar pine	40-80	3-5
Western white pine	7-20	3-7
Lodgepole pine	4-8	1
Incense-cedar	--	3-6
Western redcedar	15-25	3-4
Port-Orford-cedar	5-20	3-5
Western hemlock	20-30	2-8
Mountain hemlock	20-30	1-5

1943, Garman 1951). Cone size decreases and seed weight increases with distance from the ocean (Sorensen and Miles 1978). Seed production is often limited by cone and seed insects, which destroy practically all the seeds of certain tree species in some localities (Furniss and Carolin 1977).

Large quantities of seeds are produced by undisturbed stands during good seed years, but the proportion of each species in a seed crop does not always reflect the proportion of that species in a mixed-species stand. For example, western hemlock, Port-Orford-cedar, and western redcedar tend to be overrepresented in the seed-fall, while Douglas-fir and white fir tend to be underrepresented (Gashwiler 1969, Zobel 1979). Furthermore, environmental conditions can result in the near-exclusion of some species in favor of others (Dunning 1923).

When silvicultural treatments create a favorable environment for natural regeneration, the problem becomes one of providing sufficient seed source. Seed trees usually provide more seeds on a

regeneration site than trees in an uncut stand supply for an adjacent clearcut. Seeds from seed trees also tend to be distributed more widely than seeds from adjacent uncut stands, because the dispersal of the latter is constrained by distance. However, lone trees exposed to the wind are susceptible to windthrow (Garman 1951). Large, vigorous trees with evidence of windfirmness and past cone production should be retained if natural regeneration is to be achieved through the seed-tree or shelterwood system (Haig et al. 1941, Gordon 1970 and 1978b, Sundahl 1971, Laacke and Tomascheski 1986). Pollination is essential; because most Douglas-fir pollen falls near the parent tree (Wright 1953), excessive seed tree spacing should be avoided. Shelterwoods produce more seeds per unit area than seed trees, with less windthrow. Tree for tree, shelterwood trees also produce more seeds than the trees in an uncut stand (McDonald 1976c). They usually produce some seeds every year, even when cone crops are poor (Williamson 1973), so that it may not be necessary to schedule seed cuts to coincide with heavy seed years as long as seedbeds remain receptive (Seidel 1979, Laacke and Tomascheski 1986).

Unfortunately, seedbeds do not remain receptive very long on many sites. On these sites it may be advantageous to stimulate seed production in seed-source trees. Fertilization, root pruning, injection with gibberellin, and girdling have been used. Fertilization is ineffective in mature stands of Douglas-fir (Crossin et al. 1966), but young stands may produce more seeds if fertilized with nitrate nitrogen (Ebell and McMullan 1970). Spring applications are best, but a site-specific approach is required. Nutrient-poor sites will respond better than sites where nutrients are adequate for seed production (Edwards 1986).

Root pruning and gibberellin injections stimulate strobilus initiation in young trees (Ross et al. 1985) and may be effective in increasing the size of poor seed crops in seed orchards. Girdling seems to be more practical in the field, however, and it also stimulates the initiation of strobili during poor seed years (Ebell 1971). Girdling should be done by removing a strip of bark or cutting with a saw around half the stem circumference in two areas, one above the other, on opposite sides of the stem. Girdling should be done about 1 month before vegetative bud break. The girdle heals over

slowly without serious damage to the tree, and continues to stimulate strobilus initiation for several years (Ebell 1971). Thinning increases the size of a good cone crop in young stands but does not stimulate seed production in poor years (Strothmann and Roy 1984). Seed production seems to be stimulated by the release involved in establishing a shelterwood; bumper cone crops often develop in the third summer after creation of a shelterwood overstory (Musser 1985, Laacke and Tomascheski 1986).

### Dispersal

Conifer seeds are distributed by gravity and wind. How far and in what direction they travel depends on their weight and wing size, wind speed and direction, tree height, and even the slope of the ground in the downwind direction. Water and animals often move the seeds about later, but that initial flight from the cones is the most important factor in determining the distribution of seeds.

Siggins (1933) measured the average rate of fall in the absence of wind for seeds of 27 species. Rates varied among seed lots, but his data can be used to rank most western conifer species. Western hemlock seed falls the slowest, sugar pine seed the fastest (Figure 11-1). Therefore, hemlock seeds tend to be dispersed farther from the parent tree than sugar pine seeds. Tall trees disperse their seeds farther than short trees, however, and the increase in distance of seed flight is more than proportional to an increase in height of seed release (Isaac 1930). Furthermore, all species do not shed their seeds at the same time, and winds are seldom constant in velocity or direction. Local topography adds further irregularity to the dispersal pattern.

Seed dispersal varies from year to year and from place to place. Variations also occur due to the distribution of seed trees with respect to local topography, prevailing winds, and one another. Exposed windward slopes and the lower portions of steep slopes rising from valleys hamper effective seed dispersal (Kos 1947), and seeds from small, isolated stands cannot travel far enough to be effective. Most seeds fall within 1½ tree heights (McDonald 1980), and dispersal from a timbered edge approximates an exponential distribution as numbers of seeds decline with distance (Roe 1967). The average percentage of filled Douglas-fir seeds collected

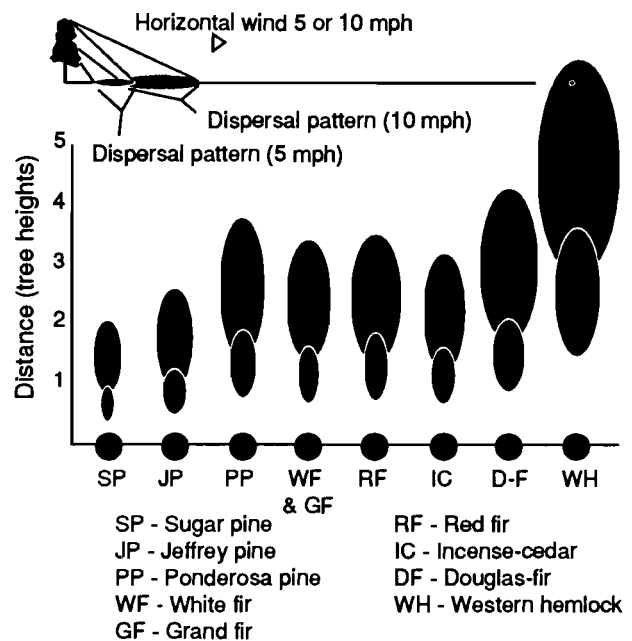


Figure 11-1. Relative seed dispersal for eight of the major species in the region. The two ellipses shown for each species approximate the pattern within which between 80 and 90 percent of the seed dropped will fall under two wind conditions. Dispersal distances were calculated from data presented by Siggins (1933) and assume a steady, horizontal wind of either 5 (smaller area) or 10 miles per hour. It is further assumed that all seeds are produced in the upper third of the tree. Actual distribution patterns may differ significantly because of shifting wind directions over the period of dispersal and turbulence.

in a clearcut at various distances from the timbered edge was 61 percent at 50 to 100 ft, 26 percent at 200 to 250 ft, and 13 percent at 350 to 400 ft (Gashwiler 1969). Similar patterns of decline occur with white fir and Shasta red fir (Franklin and Smith 1974b), western hemlock (Gashwiler 1969), mountain hemlock (Franklin and Smith 1974a), and ponderosa pine (Barrett 1966). Nevertheless, appreciable numbers of Douglas-fir seeds can be dispersed as far as a quarter-mile from an abundant seed source when the seed crop is large (Isaac 1943). Spruce and hemlock seeds can be dispersed even farther (Harris 1967).

Weight and viability of naturally dispersed seeds tend to decrease as distance from the seed source

increases. Because hollow seeds are lighter, fall more slowly, and are carried farther than sound seeds, the percentage of hollow, inviable seeds increases with distance.

Seed flight usually continues for several months (Isaac 1943, Garman 1951, Zobel 1979), and peak dispersal for individual trees varies widely (Garman 1951). Sound seeds tend to fall earlier in the season than hollow seeds, however, and the peak of viable-seed dispersion usually occurs during the first month of seedfall (Shearer and Schmidt 1970). Wind temperature and humidity have a major influence on how long it takes to complete dispersal. Cones open or disintegrate (depending on the species) rapidly in warm, dry winds, and slowly if winds are cold and wet.

Seed dispersal distance is most relevant to natural regeneration when it is considered in terms of "effective seeding distance." Roe et al. (1970) defined effective seeding distance as "the distance over which sufficient sound seed is dispersed to stock an area to an acceptable level under prevailing conditions." The distance increases as supplies of seed, wind speeds during dispersal, and longevity of receptive seedbeds all increase.

## *Survival*

Dispersed, dormant seeds are resistant to extreme temperature and moisture conditions, and the seeds of most conifer species benefit from cool, moist stratification during winter months. Nevertheless, most seeds fail to survive. Meteorological factors do not seem to be directly involved, but they indirectly affect survival by influencing the biological factors that are responsible for most of this mortality. For example, rainwater often carries seeds into holes and crannies, concealing them from seed-eaters while furnishing protected microsites where mineral soil is available (Vaartaja 1950, Tappeiner 1966). Winter snowpacks also conceal seeds from some seed-eaters; greater snow depths may have been responsible for the better spring survival observed by Minore (1986c) at high elevations. The timing of seed dispersal relative to snowfall can be important. For high-elevation true firs, the only effective seed is that which falls before the soil is covered with snow. Seeds of these species germinate on, in, and under snow, and radicles that elongate while

the seed is still several inches above ground in the snowpack desiccate and die before penetrating the soil (Franklin and Krueger 1968, Gordon 1970).

Animals eat most of the seeds in a seed crop. White-footed deer mice do the most damage, but shrews, chipmunks, and birds are also serious predators (Gashwiler 1967 and 1970). Mouse populations can recover to pre-harvest levels within 3 months after logging (Tevis 1956b), but even small populations at the time of seedfall can do much damage (Smith and Aldous 1947). Where post-harvest vegetation provides an adequate food source, these rodent populations grow much larger during the first 2 or 3 years after logging, and they respond to large seed crops by expanding even further to take advantage of the increased food supply (Hooven 1976).

Seed predators prefer certain conifer species over others. Rodents tend to prefer large conifer seeds to small ones (Smith and Aldous 1947), Douglas-fir seeds to those of lodgepole pine (Sullivan and Sullivan 1982) and western hemlock (Gashwiler 1970), and ponderosa pine and sugar pine seeds to those of white fir and incense-cedar (Beetham 1962). Most western redcedar seeds are not affected by rodent and bird predation (Gashwiler 1967).

Seed consumption tends to be most damaging when crops are small (Curtis and Foiles 1961). Indeed, rodents and birds often consume all the seeds in years of light and medium Douglas-fir seed crops. However, when a crop is small, high pre-germination mortality may reduce its size so much further that rodents and birds no longer seek it (Gashwiler 1970). A surplus is often left when there is a heavy crop (Isaac 1943). There is great spatial and temporal variation in the depredations not only of rodents but of insects and fungi as well.

## *GERMINATION*

### *Moisture, Light, and Temperature*

The critical transition from dormant seed in the soil to growing seedling is affected by many factors that vary in importance. Zlobin (1977) classified germination factors as endogenous and exogenous. Endogenous factors include a seed's



maturity, state of dormancy, size and weight, reserve nutrient capital, genotype, and inherent capacity for growth. Exogenous factors include moisture, temperature, light, aeration, soil properties, and external biological influences.

In order to germinate, the seed must imbibe moisture from its immediate surroundings. The amount needed varies among conifer species (Zlobin 1977, Thomas and Wein 1985b). The close contact between the seed and its substrate is critical in order for the seed to absorb water, but its moisture content does not have to remain constant. Indeed, a brief redrying period immediately before the seed germinates improves the vigor of the seedling (DeMatos et al. 1985). Air temperatures have relatively little direct effect on germination (Fowells and Stark 1965). The temperature of the substrate probably becomes the critical factor in stimulating germination when enough moisture is present (Haig et al. 1941). The optimum temperature for germination of most conifer seeds is 20-25°C, but sluggish germination occurs at 5-14°C (Zlobin 1977). Previous storage under cold, moist conditions increases the speed of Douglas-fir germination at 14°C and at 20°C (Jones 1961).

Long photoperiods (16 hours or longer) accelerate the germination of Douglas-fir seeds at 14°C and 20°C (Richardson 1959). The seed must be pre-conditioned by imbibing water before light has any effect on germination rate. Light intensity is relatively unimportant in the laboratory (Jones 1961), but under field conditions it does affect germination. When Strothmann (1972) germinated Douglas-fir seeds in a northern California clearcut under four shade intensities, germination was best in 65 percent shade; followed in order by 90 percent, 25 percent, and 15 percent. Under natural conditions, shade may be furnished by stumps, slash, stones, etc. (dead shade) or by surrounding vegetation (live shade). Dead shade may increase germination by reducing temperatures and conserving moisture, but those lower temperatures may delay germination in the spring (Alexander 1987). Root competition from live shade usually complicates subsequent seedling survival. North aspects provide shade and reduce temperatures on a larger scale; germination tends to occur later on north slopes than on south slopes (Strothmann 1971).

Because germinating seeds need much oxygen, waterlogged conditions impede the germination of

most western conifers. However, lack of moisture—not waterlogging—is usually the limiting factor in southwestern Oregon and northern California. Chemical composition and acidity of the soil solution do not seem to affect seed germination under normal field conditions (Zlobin 1977).

## Seedbeds

The quality of the seedbed is a primary factor in natural regeneration, because the surface on which a seed lands determines the moisture, temperature, and nutrient regimes under which germination will occur (Minore 1979, Zasada 1986). Duff, rotten wood, and mineral soil are the most common seedbeds.

Rotten wood holds moisture better than duff (Place 1950), and it does not support the competing vegetation that often inhibits natural regeneration in moist environments (Berntsen 1955). For these reasons, decayed wood is a favorable seedbed in undisturbed stands. It is also important on droughty sites in western Montana (Harvey et al. 1987). However, decayed wood is seldom a useful seedbed in southwestern Oregon and northern California because of environmental conditions there. Sufficiently decayed, well-distributed rotten wood is rarely abundant enough to cover a significant portion of the area to be regenerated. In addition, dead wood often burns before it decomposes enough to form a seedbed. The resulting charcoal stimulates early germination by raising seedbed temperatures, but its higher surface temperatures later in the season may be lethal to tender seedlings (DeKeijzer and Hermann 1966).

Mineral soil is the best seedbed for most species under most conditions. Subsurface temperatures are more extreme under mineral soil than under organic seedbeds, but surface temperatures are less extreme in mineral soil (Hermann 1963). Germination tends to be best where the mineral soil is moist and shaded (Isaac 1943, Eis 1967). Furrows and small depressions or indentations in the mineral soil promote germination (Bergman and Bergsten 1984). This benefit to germination also seems to occur on a very small scale, for coarse-textured seedbeds retain moisture beneath the large substrate particles and in crevices after other, finer-textured seedbeds have dried (Hermann and Chilcote 1965). Thermal properties of the mineral-



soil seedbed are important, and pumice seedbeds vary more in surface temperature than denser mineral soils (Cochran 1969).

The best mineral-soil seedbeds are often obtained by scarification, which benefits both germination and subsequent seedling survival (Folles and Curtis 1965). Machine-piling and burning of slash usually scarifies much of the area to be regenerated, providing ample mineral-soil seedbeds (Kovalchik and Blake 1972). Broadcast burning also exposes many mineral-soil seedbeds. Burned surfaces sometimes regenerate better than unburned surfaces, but broadcast-burning is not as effective as scarification (Steele and Pierce 1968). Moderately burned seedbeds may slightly improve the germination of Douglas-fir and western hemlock seeds (Jablanczy 1964), but only after they have been leached by rain (Gayle and Gilgan 1951). Wood ash may inhibit germination by reducing the oxygen supply (Tarrant 1954b).

Seedbed quality can be damaged when slash burning leaves local microsites severely burned. High temperatures and additions of ash and charcoal can cause detrimental physical changes in the soil that may persist for 15 years or longer (Vogl and Ryder 1969). Because severely burned surfaces have the finest particle size, contact between seed and substrate is maximized (Zasada 1986), but severe burning lowers the percolation rate, increases pH, and reduces mycorrhizal populations (Baker 1968). Fortunately, only a small percentage of most burned areas is severely burned (Tarrant 1954a). Burning does not seem to affect the eventual quantity of natural conifer stocking west of the Cascades (Morris 1970).

### *Biological Factors*

Birds and rodents constitute primary biological factors that directly influence germination success, because they consume seeds and seedlings during germination. Other biological influences affect germination indirectly by modifying the microenvironment. Mineral-soil seedbeds are created by the same gophers that destroy seedlings, for example (Tevis 1956a), and the vegetation that will compete later for soil moisture may provide live shade that benefits germination (Chilcote 1957, Gratkowski 1967). Allelopathic compounds also affect germinating seeds (Zlobin 1977), and

hardwood litter sometimes slows Douglas-fir germination under laboratory conditions, but allelopathy probably is not a primary factor affecting the regeneration of Douglas-fir in southwestern Oregon (Tinnin and Kirkpatrick 1985).

## **SEEDLING SURVIVAL AND GROWTH**

### *Moisture, Light, and Temperature*

Moisture is the most important factor limiting seedling survival and growth in most of southwestern Oregon and northern California, but adequate light and favorable temperatures are also important. All three factors are affected by silvicultural treatments.

Most mortality of naturally regenerated seedlings occurs during the first year after germination, often during the first few weeks when germinants are most susceptible to moisture stress and heat damage. Shading by an overstory canopy can reduce this mortality (Helgerson et al. 1982, Ustin et al. 1984, Selter et al. 1986). Survival is better in partial shade than in either full sun or full shade (Isaac 1943, Minore 1972b, Strothmann 1972), but shade reduces seedling growth (Day 1964, Strothmann 1972). Given adequate moisture and suitable growing temperatures (i.e. absence of heat injury or frost damage), seedlings grow best in full light (Waldron 1966, Eis 1967). When moisture is limiting, soil moisture stress may be mitigated by less-intense sunlight to produce optimal growth in partial shade (Ruth 1968), but this growth is due to the presence of moisture rather than the absence of full sunlight. Responses caused by competition for soil moisture sometimes obscure the positive effect of full light on seedling growth (Bjorkman 1944). Similarly, frost damage may negate the increased growth obtained in unsheltered, open situations.

It probably makes little difference at first whether seedlings are sheltered by live or dead shade (Thomas and Wein 1985a). Shade from invading vegetation may benefit seedling survival during the first growing season (Minore 1986c), but in subsequent seasons that vegetation will reduce seedling growth and may cause mortality by increasing moisture stress. Dead shade is better

than live shade in the long run (Isaac 1943, Minore 1971, Conard and Radosevich 1982).

Survival tends to be best on north and east aspects, poorest on south and west aspects (Alexander 1984). So far as seedling survival is concerned, there may be more of a difference between the microclimates of a north and a south slope than there is between the climate of the coast and that of the Cascades (Isaac 1943). Reductions in the density of the overstory usually benefit the survival and growth of regeneration on north and east aspects but may reduce survival on south and west aspects. Proximity to the edge of an uncut stand benefits survival in clearcuts on all aspects (Figure 11-2),

and seedlings sometimes grow more rapidly near the edge of a clearcut than they do farther away from the uncut stand (Garfitt 1966). Growth is usually most rapid along the western or southwestern edge of a clearcut, because seedlings along that edge receive sunlight during the cool morning hours and are shaded during the hot afternoons (Marquis 1965). Seedlings grown in the open, however, are usually larger than those grown under an overstory canopy (Minore et al. 1977, Harrington and Kelsey 1979); growth may be reduced when a stand edge appreciably reduces the amount of sunlight reaching the seedlings (Sims 1975). The uncut stand usually affects an adjacent clearcut for a distance of less than 2 or 3 times tree height (Gordon 1970, Caruso 1973); effects decrease with distance from the sheltering edge.

Shade stimulates height growth at the expense of diameter growth, top growth at the expense of root growth, and leaf area at the expense of strength and sturdiness (Reifsnnyder and Lull 1965). The best potential crop trees in an understory of advance seedlings may be identified by vigorous pre-release height growth, live crown ratios of 40 percent or more, and above-average crown



Figure 11-2. Abundant natural regeneration of Douglas-fir in a western Siskiyou clearcut. Note the proximity to the edge of an uncut stand.

length-to-diameter ratios (Helms and Standiford 1985, Oliver 1986).

One of the benefits of shade is that it prevents heat injury. It also delays moisture stress by slowing the drying of the soil (Thomas and Wein 1985b) and reducing water loss from leaves. Under Norway spruce shelterwoods, the rate of drying of the soil sometimes decreases with decreasing basal area of the overstory (Anders and Thomasius 1971), suggesting that effects attributed to increases in light may be partly due to increases in soil moisture. Indeed, soil moisture and leaf litter may be more important than light in affecting natural regeneration under a forest stand (Toumey 1929).

Frost damage is much more severe in clearcuts than under the canopies of partially cut stands (Williamson and Minore 1978). It is particularly serious on flat or concave topography (for example, the Dead Indian Plateau east of Ashland, Oregon) where the drainage of cold air is impeded. Frost damage varies among species: Western hemlock is the most frost-sensitive, followed by western redcedar, Douglas-fir, grand fir, white fir, sugar pine, incense-cedar, ponderosa pine, Jeffrey pine, lodgepole pine, and western white pine (Fowells and Stark 1965, Minore 1979). Removing all compet-

ing vegetation (grasses, forbs, and shrubs) reduces direct frost damage in clear-cut areas (Schneider 1969).

Frost heaving usually occurs on unshaded mineral-soil seedbeds that are exposed to the open sky at night. Late snowmelt in the spring and early snowfall in the winter reduce the length of time that frost heaving can occur (Cochran 1975), but damage tends to be most severe at high-elevation sites with low nighttime temperatures. A silty soil is most susceptible to frost heaving (Heidmann 1975), and the thermal properties of pumice soils make them particularly susceptible (Cochran 1969). Loosening or disturbing fine-textured soils increases the risk of frost heaving (Sjostrom 1944).

## *Soil*

While conifer species vary in their soil requirements, a damp, light-colored mineral soil is generally optimal for seedling survival, and duff and litter are generally detrimental. Western-hemlock seedlings grow larger on duff and litter than on mineral soil when adequate moisture is available (Sutton 1954), but most other conifer seedlings tend to grow better on mineral soil, either pure or mixed with humus, than on undisturbed litter or surface humus (Tackle and Roy 1953, Waldron 1966, Johnson 1968). The best growth usually occurs on the best soils. Nevertheless, soil is just one element in the environmental complex that influences seedling survival and growth. Moist, fertile loams and clay loams sometimes yield lower survival and poorer growth than drier, comparatively infertile sandy loams because of severe vegetative competition on the fertile soils. Furthermore, differences in growth and survival among conifer species may be reversed on different soils. For example, in trials in a growth chamber, Douglas-fir seedlings grew larger than incense-cedar seedlings on a fertile soil developed from basalt but were smaller than incense-cedar seedlings on an infertile soil developed from sandstone (Minore 1984). For seedlings of both species, survival in the field was best on the infertile sandstone soil.

The physical characteristics of a soil directly influence the survival and growth of seedlings. For example, root penetration tends to be greatest on sandy soils (Eis 1965), but the high bulk densities

and low fertility associated with exposed B<sub>2</sub> horizons limit growth (Cochran 1963). In southwestern Oregon and northern California, scree slopes and ravel layers often seriously inhibit germination, survival, and growth.

Many soil characteristics indirectly affect survival and growth by altering the amount and kind of vegetation present. Competing vegetation is often serious on productive soils (Minore 1984), and palatable vegetation sometimes encourages enough animal damage to seedlings to cause mortality as well (Cooper 1961).

Soil scarification may benefit survival and growth by creating conditions favorable for root growth (Valentine 1975) and by reducing plant competition. Where plant competition is controlled, however, the scarification and soil displacement associated with the piling and burning of slash seems to be detrimental to seedling growth (Minore 1986b, Minore and Weatherly 1990). Soil compaction associated with skid roads is also detrimental (Steinbrenner and Gessel 1955). Seedling growth is increased where scarification inverts and mixes surface organic matter rather than removing it (McMinn 1986).

Broadcast burning increases mineral-soil exposure (Smith and Wass 1976); and mineral soil may occupy almost half the burned area on sites where pre-harvest duff depths are relatively shallow (Amaranthus and McNabb 1984). Burning also releases some of the nutrients previously tied up in litter to increase available soil nitrogen in the surface soil (Vlamis et al. 1955, Wagle and Kitchen 1972).

## *Fire*

Broadcast burning of slash destroys any conifer seedlings present. Retention of logging slash may favor survival of post-harvest seedlings by providing shade and reducing soil temperatures on dark surfaces. However, seedbeds suitable for post-harvest seedlings are rare on unburned, unscarified soils. Except in coastal environments, most surviving post-harvest seedlings take root on mineral soil (Morris 1970). Soils on which slash has been burned therefore tend to have fewer advance seedlings and more post-harvest seedlings than unburned soils. Any degree of burning tends to hinder natural conifer reproduction initially

(Lavender et al. 1956). Nevertheless, stocking differences between burned and unburned areas tend to disappear in 7 to 12 years (Steen 1966, Morris 1970). Moderately intense burns probably are not detrimental.

Intensity of burning varies over a clearcut, but most areas are typically only moderately burned. The small percentage of severely burned ground most often occurs in patches where slash piles or windrows are burned. These areas are characterized by a red color and a lack of organic matter (Stewart 1978). Seedling survival is poor on severely burned soils (Vogl and Ryder 1969, McDonald 1983). Indeed, severe burning inhibits the development of almost all plant growth (Roe et al. 1970). Lowered percolation rates and fewer mycorrhizae (Tarrant 1956) may be responsible for poor seedling survival in such areas, but mycorrhizae are favored by the absence of organic matter in unburned soils (Alvarez et al. 1979), and soil moisture effects probably are most important.

Slash burning exposes mineral soil and temporarily increases the amount of water-soluble nutrients available, but its effects on conifer seedling growth vary with the environment and the severity of the burn. Shoot-to-root ratios decreased with increasing intensity of the burn when lodgepole pine and Douglas-fir seedlings were grown on burned soils in a greenhouse environment (Gayle and Gilgan 1951), but when the Douglas-fir growth was measured under field conditions in a clearcut, the ratios were higher on burned soil than on unburned soil (Valentine 1975). Leader growth is sometimes greater on moderately burned soil than on unburned areas (Haig et al. 1941). Nevertheless, burning is often detrimental to conifer seedling growth (Baker 1966 and 1968), and the damage increases with the severity of the burn. Reductions in growth may not be apparent immediately, but they become more obvious with the passage of time (Vogl and Ryder 1969). In general, however, burns of moderate intensity probably benefit natural regeneration.

### *Biological Factors*

The biological characteristics of conifer species are extremely important in natural regeneration. Shade-intolerant species are not well suited to silvicultural regimes that require regeneration in the

understory, for example, and frost-sensitive species reproduce poorly in frost-pocket areas that are clear-cut. Genetic variation within each species also affects seedling survival and growth. Lavender (1958) found that the size of Douglas-fir seeds did not affect the size and weight of the resulting seedlings, and seedling size and weight in turn were not correlated with mortality, but seedlings produced from heavy seeds survived better than those produced from light seeds. Additional variation within each species population may account for many of the differences in seedling survival and growth that occur on seemingly uniform sites.

Most sites are not truly uniform, however, and competing vegetation is an important biological factor that widens the diversity within a site. Dense vegetative cover preempts the seedbed space needed for successful germination, but young seedlings sometimes survive quite well in the shade produced by shrubs and sprouting hardwoods. Nurse-crop effects are common. In southwestern Oregon the surface soil is cooler and more moist under madrone, tanoak, and chinquapin stump sprouts than it is in the open (Minore 1986a). Manzanita and snowbrush may aid the initial establishment of ponderosa pine in central Oregon (Dahms 1950), and squawcarpet ceanothus benefits the survival of Douglas-fir and white fir seedlings on exposed sites in the Sierra Nevada (Tappeiner and Helms 1971). Light herbaceous cover favors the establishment of coniferous regeneration (Lavender et al. 1956), and mustard has been successfully used as a nurse crop on low-elevation clearcuts in western Oregon (Chilcote 1957). These beneficial effects vary with aspect, soil moisture, and soil surface temperature, however, and vegetation usually acts as a nurse crop only during the first growing season. It is detrimental thereafter, when increasingly dense growth usurps the moisture, light, and space needed by new germinants and reduces the growth of established seedlings.

Predators begin to attack seedlings soon after they germinate. Birds (for example, migrating juncos) sometimes kill the young seedlings by clipping the cotyledons as they remove suspended seed coats (Shearer 1981). Mice and cutworms can consume entire newly germinated seedlings (Isaac 1943, Roy 1983). The cutworms seem to prefer incense-cedar over white fir, ponderosa pine, and sugar pine (Fowells and Stark 1965). Rodent pop-



ulations often increase as the seedlings grow. The site disturbance associated with timber harvesting initiates an understory plant succession that seems to favor a build-up in the rodent population, particularly where slash provides cover (Alexander 1984). Warmer parts of clearcuts (centers and sunny edges) are probably preferred habitats for rodents (McDonald 1983). Gophers are a problem in some areas (Tevis 1956a), especially in clearcuts that support abundant herb cover. Gophers can completely destroy both planted and natural young conifer seedlings. Older seedlings are sometimes browsed by deer and elk.

The interactions of growth and environment tend to confound growth comparisons among species, because species respond differently in different environments. Nevertheless, the shoots of ponderosa pine, Jeffrey pine, and sugar pine seedlings grew faster than those of white fir and incense-cedar in two Sierra Nevada studies (Schubert 1956, Stark 1965). Differences in browsing damage to the white fir and incense-cedar seedlings by deer may have been responsible. Lengths of taproots and lateral roots vary with soil type and species, but seedlings of ponderosa pine, sugar pine, and incense-cedar all had longer roots than those of Douglas-fir and grand fir when grown outdoors in three southwestern Oregon soils (Stein 1978). White fir seedlings tend to have longer roots than Douglas-fir seedlings (Tappeiner 1966).

Previous growth conditions and mycorrhizae in the soil also tend to confound within-species comparisons of seedling growth. Root-growth phenology was different in natural and planted Douglas-fir seedlings on Vancouver Island; root-cell division was greatest in October for natural seedlings, but it peaked before August in the planted stock (Dunsworth and Kumi 1982). The presence of mycorrhizae on roots was associated with greater seedling weight in naturally established white fir seedlings in the north central Sierra Nevada (Alvarez et al. 1979).

Competing vegetation of any kind reduces seedling growth after the first season, but reductions vary with plant density and species. For example, the effects of manzanita are much more severe than those of snowbrush *Ceanothus* on ponderosa pine in central Oregon (Dahms 1950). Even overstory seed trees inhibit seedling growth. For ponderosa pine seed trees in northern California,

that inhibition extends outward at least 40 ft, and it persists for 4 years after the seed trees are cut (McDonald 1976b).

## SILVICULTURE

Natural regeneration is more successful near the coast than farther inland. Nevertheless, it is usually successful in Shasta red fir associations of the Cascades (Stein 1954, Gratkowski 1958). If competing vegetation is controlled, natural regeneration is usually also successful in the western hemlock series (particularly where western red-cedar is present), and in the tanoak series where rhododendron and beargrass are abundant (Chapter 5). Natural regeneration tends to be unsuccessful after clear-cutting in areas where poison-oak, hairy honeysuckle, and canyon live oak are common in the uncut stand. The canyon live oak/poison-oak and tanoak/poison-oak/hairy honeysuckle plant associations are particularly difficult to regenerate (Chapter 5).

### *Choice of Regeneration Method*

Detailed discussions of the methods used to obtain regeneration are found in Chapter 8, where artificial regeneration is emphasized. Only the effects of silviculture on natural regeneration are considered here. The choice of artificial versus natural regeneration is critical, however, and that choice should be kept in mind when selecting a regeneration method or assessing its potential effects.

Planning for natural regeneration is more difficult than planning for artificial regeneration because it is based on more numerous, more complex considerations. Those considerations include matching the biological requirements of desired species with a site's characteristics, which must be estimated from existing plant associations, indicator species, and probable responses of plant and animal populations. Planning for natural regeneration also involves assessing the influences of slope, aspect, elevation, soil type, species present, nearby seed sources, seed crop frequency, probable seed predation, future vegetative competition, and potential spread of parasites or disease to the regeneration. These ecological considerations must



Figure 11-3. Natural regeneration of western white pine, lodgepole pine, and Shasta red fir on pumice soil in a high-elevation clearcut.

be matched with management capabilities. In some cases, successful natural regeneration will depend on extending the regeneration period for a decade both to create necessary environmental conditions and to allow for the erratic nature of seed production.

Nevertheless, the extra effort and increased risk of natural regeneration are often justified by its biological and economic benefits. Natural regeneration should not be ignored because it seems difficult or has not been used recently in a given area. Forestry is changing, and the choices of tomorrow will differ from those of today, but careful consideration by qualified personnel will always be necessary. The choice of regeneration method should be based on thorough analyses by an experienced silviculturist who is familiar with local conditions. Those analyses should include the economic, social, site, species, and stand factors discussed in Chapter 8.

### Clearcut Method

The appropriate size and shape of a clearcut opening depends on the species involved, terrain, climate, prevailing wind direction at the time of

seed dispersal, and probable response of plant and animal communities to the change in environment. Clear-cuts should be small in severe environments, however, because natural regeneration is best where seedbeds are shaded by the adjacent uncut stand (Franklin 1963). Clearcut strips oriented in a north-west-southeast direction maximize this shading effect. Local conditions—including heights of the trees in adjacent stands—should determine widths of the strips, but the length of a properly oriented strip does not affect shading or seed dispersal, and acreage is not limited. The strip system lends itself well to cuttings in a planned

series (Marquis 1965), but windthrow may be a problem.

Clear-cutting favors regeneration of ponderosa pine and white fir over that of Douglas-fir and incense-cedar in the northern Sierra Nevada (McDonald 1983), and it favors regeneration of mountain hemlock over that of western white pine and Shasta red fir on high-elevation pumice deposits (Minore and Dubrasich 1981), where species mixtures are common (Figure 11-3). Competing vegetation develops slowly in the true fir type (Gordon 1979) but can be a problem on high-quality sites at lower elevations, where dense shrub growth often follows clear-cutting and broadcast burning (McDonald 1976a).

Unless abundant advance regeneration is present, seedbeds should be prepared to expose a maximum amount of mineral soil whenever that can be done without incurring unacceptable site damage such as soil compaction, removal of organic matter, or excessive heat from prescribed burning. Where advance regeneration is not abundant and soil will be compacted from the use of heavy equipment, slash should be broadcast burned. Where advance regeneration is abundant and its crown ratios and previous growth indi-

cate satisfactory growth after release, slash should be treated only if it represents a serious fire or insect hazard.

### *Seed Tree Method*

The number of seed trees necessary for natural regeneration varies with climate, seedbed, species, and seed tree quality, but 4 to 10 trees per acre are usually left (Baker 1950, Gordon 1979). Those trees should be selected for their vigorous crowns, cone-producing potential, and windfirmness. Uniform distribution of seed trees over the harvested area and adequate site preparation to create a mineral-soil seedbed are essential. In the past, suitable seed trees usually were considered too valuable to leave through a second rotation, and their removal involved some damage to the new stand. Recently developed silvicultural practices (for example, the Forest Service's New Perspectives program) include the retention of large trees for wildlife purposes, and those large trees may function as seed trees for many years. Nevertheless, the seed-tree method provides no useful modification of environmental conditions in this region, and the individual trees are subject to windthrow.



Figure 11-4. Natural regeneration of Douglas-fir under a shelterwood in the eastern Siskiyou Mountains.

### *Shelterwood Method*

The shelterwood method can be used successfully with most species in most environments if one is willing to accept longer regeneration periods and a reduction in understory growth. This growth reduction may be caused by competition for available soil moisture from overstory and understory vegetation as well as by decreased light (Hobbs and Owston 1985). Nevertheless, natural seedlings are often abundant (Figure 11-4), and the shelterwood method should be considered wherever clear-cutting would result in unacceptably harsh conditions for natural regeneration (e.g., frost pockets or hot, dry south slopes). Overstory basal areas of 50 to 100 ft<sup>2</sup> per acre are usually sufficient (Williamson 1973, Seidel 1979), but optimal overstory densities vary with the species and the site. The number of overstory trees should be determined by the degree of site amelioration desired and the problems anticipated during overstory removal. Overstories should increase in density with shade tolerance of the species and the need for shelter (e.g., aspect, slope, and frost hazard). They should consist of well-formed dominant or co-dominant trees

of the species to be regenerated. Site preparation to expose a mineral-soil seedbed will improve stocking and shorten the regeneration period. Vigorous advance regeneration of the desired species should be preserved.

Removal of the overstory is critical to release of advance regeneration. The average dbh and the total longitudinal cross-sectional area of the overstory trees can be used to estimate the post-harvest stocking that will remain after a shelterwood overstory is removed from an area with adequate regeneration (Laacke and Fiddler 1986). Damage to that regeneration is minimized by marking the



seedlings that are to be saved, laying out skid trails and cable corridors in straight-line patterns before the sale is advertised, designating felling beds, designating rub trees or cull logs along the edges of skid trails to protect the regeneration, and yarding directly across contours (Fiddler and Laacke 1985, Tesch et al. 1986; see also Chapter 9).

### *Selection Methods*

When management objectives are to protect streams or enhance aesthetic values (for example, to screen a campground), selection may be the regeneration method of choice (Gordon 1978a). Administrative costs are high, however, and using selection to establish and maintain an all-aged stand is economically justifiable only where an excellent road system, gentle topography (suitable for tractor yarding), and a nearby market make repeated stand entries feasible. Selection provides nearly optimal conditions for the natural regeneration of many species. Seed-crop periodicity is usually not a problem. Single tree selection is best suited to shade-tolerant species, however, and seedling growth is usually less than that attained under even-aged systems. Group selection should be used when uneven-aged management is applied to shade-intolerant species.

### *Culture of the New Stand*

Natural regeneration is inherently irregular, and local areas of over- and understocking are likely to occur. Therefore, precommercial thinning and supplemental planting are often necessary to obtain a uniform stand. Under suitable conditions it may be possible to combine these operations by transplanting young seedlings from patches of dense regeneration to nearby understocked areas (Carlquist 1950). Another method might be to create naturally seeded nursery beds in small, scarified clearcuts with the purpose of transplanting the resulting seedlings into nearby harvested areas (Armit 1969); this procedure needs further testing. Precommercial thinning and supplemental planting are expensive however they are accomplished. This added expense should be considered whenever the economics of natural and artificial regeneration are compared.

## **SUMMARY**

Under present management constraints and economic objectives, natural regeneration is seldom used in most of southwestern Oregon and northern California. Natural regeneration is cheaper than artificial regeneration where it can be used successfully, however, and it guarantees adaptation of the seedlings to the site. Furthermore, present practices are rapidly changing, and increasing emphasis on programs like the Forest Service's New Perspectives are making natural regeneration more applicable.

Successful natural regeneration is difficult to obtain on many sites. It often involves long, uncertain regeneration periods. Seed production is erratic but generally sufficient if vigorous, seed-bearing trees are reserved to provide seeds in environments favorable for their germination and for the survival of the seedlings. Favorable environments include adequate substrate moisture and moderate temperatures that benefit both the establishment and the subsequent growth of seedlings. All the commonly used regeneration methods may be used to obtain natural regeneration, but prompt, abundant seedling establishment becomes more certain as one progresses from small clearcuts through seed trees and shelterwoods toward selection. The wide variety of specific site conditions, biological limitations, and management objectives makes it difficult to define sites where natural regeneration should be used. Nevertheless, a few generalizations apply throughout most of southwestern Oregon and northern California.

Natural regeneration tends to be most successful on moist sites. The general distribution of growing-season moisture in southwestern Oregon and northern California has been described (Major 1977, McNabb et al. 1982). Site-specific moisture conditions can be estimated by using indicator plants in several areas (Griffin 1967, Minore 1972a, Graham et al. 1982, Minore et al. 1982 and 1984). Where moisture is not limiting, poorer soils tend to be more suitable for natural regeneration than more fertile soils. Slightly acid soils seem to be better than soils of higher pH (Grunda 1972). Soil depth and field capacity are positively correlated with natural regeneration success; percent rock content is negatively correlated (T. Atzet, personal communication).

High-elevation sites tend to be suitable for natural regeneration only on sloping ground without frost pockets. Frost damage often makes flat or concave topography unsuitable after the overstory is removed, and the risk of frost damage increases with elevation. At lower elevations, regeneration under residual overstory trees tends to be best on south and west slopes. Regeneration after clear-cutting is best on north and east slopes. When other variables are equal, stocking tends to decrease as slopes become steeper.

Where all other factors are equal, there is less economic justification for investment in artificial regeneration on poor sites than on good sites. The poor sites tend to favor methods that pay regeneration costs through reduced revenues and delay rather than as a cash outlay (Brodie 1985), and most natural regeneration costs are expressed as delays or reduced revenue.



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