CONSTRAINTS ON CONIFER REGENERATION: A REVIEW OF THE LITERATURE AND A CONCEPTUAL MODEL FOR THE PACIFIC NORTHWEST REGION

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INTRODUCTION

The rate at which conifers regain dominance after large-scale disturbance has important implications for many aspects of forest ecosystem development. Levels of biological diversity, trophic interactions, and numerous ecosystem processes (e.g., carbon storage, water and nutrient cycling) are directly or indirectly affected by the pattern and pace and of succession. In the Pacific Northwest, there is abundant evidence that following stand-replacing disturbance (whether natural or of human origin), rates and densities of conifer regeneration can vary markedly among sites (e.g., Franklin & Hemstrom 1981, Nesje 1996, Tappeiner et al. 1997, Poage 2001, Winter 2000). A central objective of the Early Succession Synthesis Area is to quantify the consequences of this variation for carbon stores, soil properties, and biological diversity in plantations in and around the Andrews Experimental Forest. Clearly, for particular components of the forest (e.g., tree biomass), effects of variable rates of regeneration are very clear; however for other ecosystem components (e.g., understory biomass, soil properties), effects have been more subtle or difficult to detect (e.g., unpublished LTER reports by Griffiths et al. 2001 and Bisbee et al. 2001).

Ultimately, if we can identify the biotic and/or abiotic correlates of this variation, it should be possible to model landscape-scale responses to spatial variability in regeneration, and to predict local or larger-scale consequences of a change in climate, disturbance regime, or forest management. To this end, we have begun to review the large body of literature that addresses the general question, "what factors influence rates of conifer establishment, survival, and growth after stand-replacing disturbance?" (see annotated bibliography in Appendix A). Given the applied context of the problem posed in Synthesis Area B, we have focused this review largely on the "forestry" literature, which includes retrospective surveys of post-harvest regeneration, silvicultural experiments and regeneration trials, and related studies from within the Pacific Northwest region (British Columbia to northern California). Although there is an additional literature on conifer invasion of meadows, old fields, and powerline rights-of-way, we limit consideration of that work, because our focus is on failure of planted trees, not of naturally establishing seedlings. However, in sum, this work suggests that a diversity of biotic and abiotic factors can act singly or in concert to shape regeneration patterns, and the relative importance of these factors can vary markedly in space (i.e., with changes in physical/biotic environments) and time (i.e., with changes in climate and forest management practices).

In the pages that follow, I provide a brief overview and synthesis of this literature (but see Appendix A for summaries of individual studies). With the goal of providing a framework for future retrospective or experimental research in LTER, I conclude with a general conceptual model of the processes that influence the rates and patterns of post-harvest regeneration with an emphasis on those factors most relevant to our region (western Oregon).

CONSTRAINTS ON CONIFER REGENERATION

In the most general terms, constraints on successful regeneration (and ultimately, on stand development) may occur at several stages in the life history of a conifer. Illustrated below, these constraints operate to limit transition from one life stage to the next:

[*1*] [*2*] [*3*] [*4*]
seed production → seed dispersal → post-dispersal seed survival → germination →
1st -yr seedling → "established" seedling/sapling
[*5*] [*6*]

It seems reasonable to assume, however, that the factors that might prevent transitions between stages [*1*] and [4] have limited relevance to our current work in plantation forests. Since the mid-1960s, most harvest units have been hand planted with 1- to 2-yr-old seedlings. Although natural regeneration may contribute substantially to stand regeneration in managed forests, the general expectation is that sufficient stocking can be achieved by planting alone. Thus, the current review focuses on those factors that affect survival and growth of outplanted seedlings and therefore considers only stages [*5*] and [*6*]. For simplicity, these factors can be generally grouped as: (1) abiotic variables (including physical environment, microclimate, and edaphic effects); (2) biotic variables (including effects of consumers, competitors, and facilitators); and (3) variables related to site preparation and reforestation techniques.

1. ABIOTIC EFFECTS

Explanations for variable rates of conifer establishment and growth are most commonly associated with effects of:

- Aspect and slope (as they influence solar radiation, air and soil temperature, and evapotranspiration);
- Elevation (as it influences air and soil temperature, length of growing season, annual precipitation, and snow depth and persistence); or
- Landform and topography (as they interact with aspect and slope to influence solar radiation, temperature, soil moisture availability, and potential for frost)

A review of the literature from the Pacific Northwest, suggests, however that these effects are not fixed, but that they vary in magnitude as functions of latitude (from British

Columbia to southern Oregon) and longitude (e.g., with distance from the coast). However, we can make some generalizations:

1.1. Aspect

In much of the PNW region where growing seasons are long and summer drought is common, conifer establishment following harvest is often more difficult to ensure on S- and W-facing slopes than on N- and E-facing slopes (e.g., Seidel 1979, Strothmann 1979, Graham et al. 1982, Minore et al. 1982, Ferguson et al. 1994). Mortality of planted seedlings is often attributed to excessive temperatures (increasing evaporative demand and photorespiration) and/or insufficient soil moisture (Cui and Smith 1991). However, S- and W-facing slopes may not present the same impediments to establishment in more coastal locations (e.g., the Oregon Coast Range), at higher elevations (e.g., silver fir zone), or at more northerly latitudes (northern Washington and British Columbia) where summer drought is less common, precipitation is greater, or snowpacks are deeper and more persistent (see below). In fact, under these situations, S and W aspects may be more conducive to successful regeneration (e.g., Farnden 1994). A similar pattern can be observed in subalpine meadows, where natural establishment of conifers is limited by the persistence of late-lying snowpacks on N and E-facing slopes, but less so on S- and W-facing slopes (e.g., Rochefort et al. 1994, Miller and Halpern 1998).

1.2. Elevation

1.2.1. Temperature. Effects of elevation are manifested primarily through gradients in temperature (declining with elevation) and snowpack (generally increasing with elevation). Physiological processes (including transpiration, photosynthesis, and root growth) are controlled, in large part, by air and soil temperature. Early in the growing season, low soil and air temperatures inhibit water flow through the soil-plant-air continuum, and can induce water deficits even when soil moisture is not limiting (see review in Farnden 1994). Effects can be seen on root, stem and needle growth. Because air temperatures increase more rapidly through spring and summer than do soil temperatures, low soil temperature appears to be the main factor limiting seedling growth at higher elevations. In addition, temperature-induced water deficits that occur late in the growing season may adversely affect the onset and depth of plant dormancy. All of these effects are more common on N- and E-facing slopes than on S- and W-facing slopes.

1.2.2. Frost. Seedling survival can be limited by frosts that result from radiative cooling (usually on cold, clear nights). The likelihood of radiative frost (in contrast with advective or down-slope movement of cold air) increases with elevation. Advective frosts, by contrast, can occur at many points on the landscape and at a variety of spatial scales (e.g., in a small depression, behind the downslope edge of a clearcut, or in a valley bottom). Here, the risk of large-scale frost may be greater at lower elevations as cold air drains from mountain slopes into major valleys (Farnden 1994). In general, the risk of damage is greatest when seedlings are small (as temperatures are coldest near the ground surface), and are most pronounced during the year of planting (Stathers 1989).

1.2.3. Snow. Both the amount of snowfall and the persistence of snowpacks tend to increase with elevation. Snow can influence seedling survival through its effect on thermal and soil moisture regimes. Late melting snow may inhibit soil warming and reduce the effective growing season for seedlings. Snow can also cause direct physical damage to tree seedlings (Leaphart et al. 1972) by flattening stems and branches or trapping seedlings beneath mats of associated vegetation. Species with very different growth forms, branch structures, and stem resilience have varying capacities to tolerate burial and snow creep. Clearly, the potential influence of snow increases with elevation and with the magnitude and duration of snowpack.

1.3. Landform and Topography

As discussed above, landform and topography can exert major controls on seedling survival and growth through their influences on solar radiation, soil moisture availability, snow accumulation and persistence, and the potential for radiative frost.

2. BIOTIC EFFECTS

A diversity of biotic factors can limit the post-harvest establishment and growth of conifers. These include:

- Herbivory by large ungulates (deer, elk), cattle (in some locations), fossorial mammals (pocket gophers, mountain beavers), rabbits/hares, and insect pests (cutworms, root collar weevils)
- Competition with post-harvest residual and early seral vegetation
- Mycorrhizal limitations, fungal pathogens, and phytotoxic effects

2.1. Herbivory

Effects of herbivores on conifer establishment can vary from relatively minor reductions in height growth (e.g., McDonald 1983) to major effects on seedling survival. Damage to small or recently planted seedlings can result in mortality (Teipner et al. 1983, Stein 1995). Herbivory can occur year-round (even when seedlings are buried by snow). Susceptibility to herbivores can vary with habitat (e.g., mountain beavers are most commonly found in moist habitats) or geographic location (e.g., in areas that support higher densities of deer and elk), and in time, as population densities of large mammals fluctuate.

Insect damage (e.g., from cutworms and root collar weevils) can also contribute to mortality of small seedlings (Gashwiler 1971, Arnott et al. 1995), although effects appear to be local and not easily predicted.

2.2. Competition

There is a large and diverse literature that addresses the role of competing vegetation in the establishment and growth of tree species following forest harvest (e.g., Haeussler and Coates 1986, Stewart et al. 1984, Cole and Newton 1987, Newton and Preest 1988, Coates et al. 1991, Farnden 1994, Stein 1995, Whitehead and Harper 1998). Competition can occur for growing space, light, soil moisture, and/or soil nutrients, and the source of competition can range from residual understory species that show vigorous vegetative reproduction (e.g., vine maple, salal, bracken fern), to early seral species that originate from the soil seed bank (e.g., Ceanothus spp., Arctostaphylos spp., Rubus spectabilis) or whose seeds disperse by wind (e.g., alder, fireweed, and grass species) (see reviews in Haeussler and Coates 1986). Trees are particularly susceptible to competition-induced mortality and growth depression while they remain subordinate. Consequently, "vegetation management" efforts (e.g., brushing and herbicide applications) are typically applied soon after harvest.

To some extent, the potential for a particular vegetation type to present a "competitive challenge" to regeneration, can be predicted from understory composition prior to harvest. For example, in low-elevation coastal sites in B.C., salal-dominated understories can limit successful regeneration (Haeussler and Coates 1986). In the western Cascade Range, understories with heavy dominance of vine-maple may present similar obstacles to successful establishment and growth (Halpern, pers. obs.). However, the potential for early seral species to compete with regenerating trees may be less predictable, as these species are often dependent on an *in situ* seedbank (e.g., Ceanothus spp.) whose presence and relative abundance vary considerably in space and time (e.g, Halpern 1989).

In addition to direct competition for light and soil resources, "competing" vegetation may also exert indirect effects on tree survival via "snow press"— the compression of small seedlings through snowloading of overtopping vegetation (Farnden 1994)—or through reduction of soil temperatures by shading (Brand 1991, Coates et al. 1991).

Although there is a tendency to assume that post-harvest understories exert only a negative effect on seedling establishment and growth, there is considerable evidence that under some conditions (particularly when environmental stress is high) herbaceous and woody plants may facilitate seedling survival and growth (e.g., reviews in Conard et al. 1985, Farnden 1994). For example, ground-layer vegetation may (1) protect seedlings from growing season frosts (e.g., Stathers 1989, Steen et al. 1990) or excess solar radiation (reviews in Conard et al 1985, Farnden 1994); (2) improve soil physical and chemical properties through additions of organic matter and biologically fixed nitrogen (e.g., N-fixation by *Ceanothus* spp.); (3) stabilize soils on steep slopes; (4) protect seedlings from insect and browse damage; or (5) serve as alternate hosts for desirable mycorrhizae (see next section).

2.3. Mycorrhizal Limitations, Fungal Pathogens, and Phytotoxic Effects

The importance of ectomycorrhizal (ECM) fungi to establishment and survival of tree seedlings is well established (Amaranthus and Perry 1987). The persistence of ECM fungi through catastrophic disturbance usually depends on the persistence or rapid reestablishment of potential host plants. In forests of the Pacific Northwest, seedlings of Pinaceae share ECM with many woody, ericaceous species (e.g., *Arctostaphylos*, *Arbutus*) which are abundant seedbank colonizers or resprouters following forest harvest (Amaranthus and Perry 1994). These alternate mycorrhizal hosts provide the link between old and new tree populations and thus may indirectly facilitate, rather than inhibit, seedling establishment and growth. It has been hypothesized that under particularly harsh conditions, where native plant species are removed or lost as a consequence of forest management activities, synergistic or positive feedbacks can result, leading to soils depleted in nutrients, organic matter, water holding capacity, physical structure, and native biota (Perry et al. 1989).

ECM persistence through disturbance is limited by many factors. In dry or cold (e.g,. boreal) climates persistence may be limited by spore production, germination, and mycelial growth, reducing the likelihood that tree seedlings will be colonized. Severity of forest management practices may also be important. For example, studies of Wright and Tarrant (1958), Parke (1982), Parke et al. (1984), and Amaranthus et al. (1989) suggest that ECM formation in burned clearcuts (and particularly in severely burned sites) can be greatly reduced relative to undisturbed or unburned soils (although work of Pilz and Perry [1984] and others suggests that ECM innocula potential may not be influenced by intense fire). Coarse woody debris and soil organic matter retained through harvest are also important for ECM persistence, as fungi predominate in woody debris and organic soil layers. Finally, if post-harvest vegetation becomes dominated by VA or nonmycorrhizal species—for example through seeding of annual grasses to mitigate for soil erosion—ECM fungi may be replaced or lost, resulting in reduced survival and growth of conifer seedlings. It has also been suggested that under excessively dry, post-harvest conditions, expansion of actinomycete populations (which are tolerant of environmental extremes), may limit ectomycorrhizal formation through exudation of inhibitory chemicals (Perry and Rose 1983, Friedman et al. 1989).

Other biotic causes of mortality/suppression of conifer seedlings include the phytotoxic effects of some vascular plants (e.g., bracken fern [Ferguson and Boyd 1988]) and actinomycetes (Friedman et al. 1989), infection by blister rusts (e.g., Arnott et al. 1995), and the effects of root pathogens, including A*rmillaria mellea* and *Phellinus weirii* (Filip 1979), *Heterobasidion annosum* (Filip 2000) and *Cylindrocarpon* and *Fusarium* spp. (Axelrood et al. 1998).

3. SITE PREPARATION AND REFORESTATION TECHNIQUES

Post-harvest site preparation and planting practices may have significant effects on seedling survival and growth. There can be simple, direct explanations for planting failure. For example if nursery stock is of poor vigor or harbors root rot organisms (*Cylindrocarpon, Fusarium*) at the time of outplanting, survival can be reduced (Axelrood et al. 1998). Similarly, compared with bareroot seedlings, container-grown seedlings often perform poorly because of limited development of root systems, greater susceptibility to careless handling/planting, frost heaving, or animal damage (Gutzwiler and Winjum 1974, Tinus and Owston 1984).

The ways in which logging residues are treated may play a central role in the success of planted seedlings. Historically, in the Pacific Northwest, broadcast burning of logging slash had been applied routinely to reduce future fire hazard, to facilitate planting, and to reduce the abundance of shrubs that compete for light and below-ground resources. Under conditions of deep and dense slash, burning to reduce fuel loadings may ensure that there are adequate "spots" for planting. However, intense burns that remove most or all potential sources of shade, that reduce future inputs of organic matter and nitrogen, that result in greater soil instability or permeability, or that remove obstacles to browsing by deer or elk, can create stressful abiotic or biotic environments for newly planted seedlings. There is abundant evidence that mortality ascribed to excess solar radiation or moisture stress, frost damage, or loss of mycorrhizal inoculum (e.g., Minore et al. 1984, Ferguson et al. 1994, Strothmann and Roy 1995), can be traced to "improper" site preparation techniques, rather than to the intrinsic environmental conditions of particular regeneration sites. Clearly, the detrimental effects of overly intensive site-preparation practices are more likely to be observed at more southerly latitudes and on steep, south-facing slopes.

A CONCEPTUAL MODEL

A large body of literature clearly points to the diversity of factors that can shape patterns of conifer establishment after stand-replacing disturbance. However, a major challenge lies in understanding how the magnitude and direction of these effects (and their interactions) vary in time and space. In an attempt to capture this complexity, I have developed a simple, conceptual model of the biotic, abiotic, and management-related factors that shape seedling survival in forests of the Pacific Northwest (Fig. 1). In the context of future work in LTER, this model serves a number of purposes:

- it can be used to structure our thinking about the multivariate nature of controls on conifer establishment;
- it can guide future efforts to quantify gradients in conifer establishment and stand development, by suggesting a stratification scheme for sampling the landscape.
- it can be used to frame hypotheses about the mechanisms that limit conifer survival and to suggest manipulative experiments that test these hypotheses.

Ultimately, if we can quantify the sources of variability and identify the mechanisms that underlie successful conifer establishment, we can model landscape-scale patterns of regeneration and predict responses to changes in climate, disturbance regime, or forest management.

In simple terms, this model identifies three general classes of variables: biotic and abiotic, and those related to forest management (Fig. 1). These are often represented by broad classes of "variables" whose influences (line arrows) are expressed through more proximate mechanisms (broad arrows). For example, the effects of elevation are manifested as gradients in air and soil temperature, precipitation, snow depth and persistence, and the likelihood of frost. Similarly, the effects of aspect are manifested in gradients of solar radiation and temperature and indirectly in how these influence snow persistence. There can also be interactions among and within these broad classes of variables (single- and doubled-headed line arrows). For example, effects of aspect can be moderated by elevation (on S-facing slopes soil moisture may be less limiting at higher elevations). Likewise, vegetation cover can have a positive influence on susceptibility to frost, and site preparation can indirectly affect seedling survival through direct effects on competing vegetation.

However, the relative importance of each of these direct and indirect effects can vary substantially across the landscape. As a consequence, particular factors may increase or diminish in importance, may switch from exerting a positive to a negative effect (or vice versa), or may become irrelevant entirely. I illustrate this complexity by presenting three hypothetical models that represent distinctly different physical settings in the Pacific Northwest: low elevation, south-facing slopes in the western Cascades (Fig. 2); high elevation, north-facing slopes in the western Cascades (Fig. 3); and south-facing slopes in the Siskiyou Mountains of southwestern Oregon (Fig. 4).

Low elevation, south-facing slopes in the western Cascades (Fig. 2).— Solar radiation and temperature (as they influence soil moisture availability, evapotranspiration, and photorespiration) exert major controls on seedling survival (large "-" effects). These effects can be moderated or exacerbated by topography ("+/-" effects) or by site preparation activities that remove organic horizons or CWD ("+" effects on solar radiation and temperature). Similarly, given the likelihood of summer drought in this environment, timing of planting and vigor of planting stock can have important consequences for seedling survival ("+/-" effects). Additional indirect effects include the potential benefits of shading by residual vegetation ("-" effects on solar radiation and temperature). Other biotic and abiotic factors are assumed to exert comparatively minor controls on seedling survival.

High elevation, north-facing slope in the western Cascades (Fig. 3).— Here, snow depth and persistence ("-" effects), as well as temperature and solar radiation ("+" effects) exert major controls on conifer regeneration (note the switch from "-" to "+" for temperature and solar radiation compared to Fig. 2). The potential for radiative frost also becomes apparent at higher elevations ("-" effect). Competing vegetation exerts both a negative direct effect, and potentially, a positive, indirect effect by moderating the potential for frost damage. Given the shorter growing season available at high elevation, late snow-lie sites, timing of planting and seedling vigor are also important determinants of successful establishment. Herbivory is assumed to play a limited role in seedling survival compared to environmental constraints (absence of an arrow).

South-facing slopes in the Siskiyou Mountains, southwestern Oregon (Fig. 4).— Similar to low elevation, south-facing slopes in the western Cascades, solar radiation and temperature have the potential to exert strong negative effects on conifer survival in southern Oregon. Compared to more northerly latitudes (w. Cascades), lower annual precipitation can also constrain seedling survival and growth ("-" effect of [reduced] precipitation). Elevation can moderate the influence of limited precipitation through orographic effects (indirect "+" effect of elevation). There is also considerable evidence that ectomycorrhizal (ECM) fungi play a critical role in this region and that intensive management practices (broadcast burning) can sever the link between seedlings and fungi: (1) through direct consumption of the soil organic layers and CWD in which fungal mycelial are most abundant ("-" effects on ECM fungi), or (2) by killing "associated vegetation", e.g., ericaceous shrubs, that serve as alternate hosts as conifers become established.

Although it is possible to develop similar, hypothetical models for numerous other points in the Pacific Northwest landscape, these examples illustrate some of the sources of variation. However, they also highlight uncertainties in our understanding. For example, it is unclear how herbivory or competitive interactions vary in magnitude along major environmental or geographic gradients. There may be consistent relationships that can be modeled, but there are also likely to be stochastic effects (e.g., related to temporal fluctuations in animal populations, or to site disturbance history). Additional sampling at larger spatial and temporal scales may improve our understanding of these relationships.

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