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ARRESTED SUCCESSION IN OLD FIELDS WITHIN A TEMPERATE RAIN FOREST

Dennis Alan Riege

A dissertation submitted in partial fulfillment of the
requirements for the degree of

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Abstract

Arrested Succession in Old Fields within a Temperate Rain Forest

by Dennis A. Riege

Chairperson of the Supervisory Committee:
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Vegetation of old fields in the temperate rain forest of the Queets River Valley, Olympic National Park, Washington, USA remains dominated by exotic herbs 60 years after abandonment. Exploratory vegetation analyses revealed that seven species dominated the old field vegetation: the persistent European pasture grasses *Agrostis gigantea* and *Anthoxanthum odoratum*, and five species that have invaded since abandonment: the exotic *Cirsium arvense* and *Rubus laciniatus*; and the native *Carex obnupta, Pteridium aquilinum*, and *Picea sitchensis*. The expanding patches of *Cirsium*, *Carex*, and *Rubus* appeared to be successional changes that will not lead to tree establishment. Tree colonization by *Picea* is more probable in fields that have older alluvial soils with higher organic matter, moisture and acidity; were burned prior to clearing; and were less disturbed by past agricultural use.

Study of field edges revealed that invading *Picea* seedlings were virtually limited to older soils that had *Anthoxanthum* or *Pteridium* cover. The most important soil and cover factors to *Picea* invasion were *Agrostis* cover (negative correlation) and soil organic matter (positive correlation). *Agrostis* formed sod and increased ground cover, which may inhibit *Picea* seedling establishment.

In experiments with sown seeds, seedlings of *Picea* and *Tsuga heterophylla* emerged as readily in *Agrostis* as in *Pteridium* or *Anthoxanthum*, but suffered higher mortality in *Agrostis*. Seedling establishment was very low in all cover types and almost nonexistent without experimental reduction of competing vegetation. Exclusion of rodents increased seedling emergence in some sites but not others. Cervid herbivory suppressed growth of *Tsuga* and *Alnus rubra*, both on transplanted seedlings outside of fenced exclosures and on natural seedlings in permanent plots. In contrast, *Picea* was not browsed and grew steadily in height with little mortality. Growth of *Picea* seedlings may be facilitated by *Pteridium*.

Picea, *Tsuga*, and *Alnus* have small seeds and are poorly adapted to establishment in dense vegetation. Competition appears to be the prime inhibitor of tree colonization; it may be intensified by *Agrostis*, the most abundant cover type on the fields, and by the dry summers of the Pacific Northwest. If past and present dynamics continue, succession of most of the meadows to forest may be arrested indefinitely.

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1. INTRODUCTION

One hundred and one years ago, the publication of the perceptive work of Cowles (1899) on temporal changes in vegetation of Lake Michigan sand dunes brought succession to the forefront of the young science of ecology. Although Cowles recognized succession as a complex process ("a variable approaching a variable rather than a constant," Cowles 1901), the deterministic theories of Clements (1916) of a linear progression of communities to a climatically-determined climax became the "classical succession paradigm" (McIntosh 1999) that dominated ecology for several decades. In the last half of the 20th century, theories of plant succession shifted emphasis from the Clementsian view to those that incorporate individualistic species behavior, population dynamics, and stochastic events (Gleason 1926, Egler 1954, Noble & Slatyer 1980). For the past quarter century, an experimental approach that examines the mechanisms of succession has been favored (Connell & Slatyer 1977, Pickett et al. 1987, Glenn-Lewin et al. 1992).

Abandoned agricultural fields long have been used by ecologists as a model system to examine processes of secondary succession. Early studies were in the eastern USA, where old fields typically progressed from pioneer herbaceous species to shrubs and trees in a few decades (Billings 1938, Keever 1950, Bard 1952, Beckwith 1954). This produced a Clementsian view of old field succession that is commonly presented in textbooks to exemplify secondary succession (Odum 1959, Smith 1992, Krebs 1994). More recent studies have pointed out individualistic patterns in old field succession (Pickett 1982, Keever 1983).

An experimental approach to the study of mechanisms that affect tree colonization during old field succession has been applied by several workers. De Steven (1991a, 1991b) in North Carolina and Gill & Marks (1991) in New York published comprehensive, multifactorial studies of tree seedling establishment in old fields. These and other experimental studies showed that tree colonization can be inhibited by seed and seedling predation by rodents (De Steven 1991a, Gill & Marks 1991, Myster & Pickett 1993, Ostfield & Canham 1993), competition from herbs (De Steven 1991b, Gill & Marks 1991, Berkowitz et al. 1995, Prach et al. 1996), cervid herbivory (Myster & McCarthy 1989, De Steven 1991b, Hill et al. 1995, Lawson et al. 1999), or scarce resources (Myster & McCarthy 1989, De Steven 1991b). Tree establishment also can be facilitated by herbs (De Steven 1991a, Gill & Marks 1991).

Mechanisms can interact. For example, one species may have both facilitative and inhibitory effects on another species (del Moral & Wood 1987, Walker & Chapin 1987). Callaway & Walker (1997) suggested that the balance between facilitation and competition can be tilted by factors such as abiotic stress or the life histories of the interacting species. In a review of tree colonization of old fields, Myster (1993) concluded that successful invasion depends primarily on seed predation, seedling predation, and competition. He considered these processes, which involve interactions among species or between species and environment, to be more essential than non-interactive life-history traits. The relative importance of these mechanisms probably differs with environmental variation within and among old fields. Studies that examine the effects on mechanisms of local differences in plant cover or soils are uncommon (but see Myster & Pickett 1989, Burton & Bazazz 1991, Berkowitz et al. 1995).

Old fields abandoned over 60 years ago in the Queets River Valley of Olympic National Park (ONP) show little invasion by trees, yet they are surrounded by rain forest. This contrasts with the preponderance of old-field studies in temperate forest biomes that report woody plant invasion in 20-30 years (Keever 1983, Falinska 1991, Myster 1993, Smit & Olff 1998). The moist climate and fertile soils of the Queets fields also differ from the nutrient-poor, xeric conditions associated with the few examples of old fields that have persisted for over 50 years (Inouye et al. 1987, Osbornova et al. 1990, Prach et al. 1996). Rates of old field succession within localities can vary (Osbornova et al. 1990, Myster 1993, Myster & Pickett 1994). Rates can be influenced by soil nutrient status (Tilman 1988), competition (Prach et al. 1996, Smit & Olff 1998), or herbivory (Davidson 1993, Lawson et al. 1999).

The central objective of my study was to answer the question: "why have trees failed to colonize most of the Queets fields?" Since trees, primarily *Picea sitchensis*, now occupy parts of some fields and seedlings are invading some field edges, my question became more general: "how do environmental differences among old fields affect tree invasion?"

The Queets old fields are dominated by exotic species. The persistence of nonnative species threatens the mission of national parks to preserve natural ecosystems (MacDonald et al. 1989, Westman 1990). Since my study involves mechanisms of colonization of nonnative vegetation by native trees, my results are pertinent to park managers interested in restoration of native communities.

In Chapter 2, I describe the ecological and historical context of the study fields. I also track the history of invasion of the fields by four non-tree species, as determined primarily from aerial photographs.

Chapter 3 includes descriptive studies of the growth and survival of natural tree seedlings that established along field edges. Individuals were monitored for two growing seasons in permanent plots. In addition, I examine the establishment and crown growth of trees over the past 60 years from sequential aerial photographs.

Exploratory vegetation analyses are reported in Chapter 4. Vegetation and soil data were collected during 1997 and 1998 in extensive surveys of 11 fields. These data were subjected to indirect and direct ordination and other correlative analyses to generate hypotheses about the factors that affect tree invasion. Several of these hypotheses are examined in subsequent chapters.

Chapter 5 encompasses a study of *Picea* seedling invasion of selected edges. Relationships of vegetation and soil factors to *Picea* invasion are investigated in more detail and at a finer scale than in Chapter 4.

In Chapter 6, I report a series of experimental studies on the effects of competition and seed predation on tree seedling establishment from sown seeds, as well as the effects of cervid herbivory, competition, and facilitation on survival and growth of transplanted seedlings. The relative importance of these effects is compared among different cover types.

The results of these studies are synthesized in Chapter 7, including suggested practices that can be used by park managers who are concerned about restoration of fields to native forest.

2. DESCRIPTION OF STUDY FIELDS AND HISTORY OF THEIR INVASION BY FOUR SPECIES

Study Areas

My study examined succession in abandoned agricultural fields that are located along 15 km of the Queets River within Olympic National Park (ONP), Washington, during 1996 to 2000.

Beginning in 1890, scattered homesteads were established along the Queets River (Alcorn & Alcorn 1973). Many settlers chose sites near the river that were occupied by riparian hardwoods or that had burned in the 1890s. The fields were used primarily for pasture (cattle, sheep, or horses), hay, and oat crops (Williams 1975). Species most commonly utilized for hay and pasture included *Agrostis gigantea, Holcus lanatus, Phleum pratense, Dactylis glomerata, Trifolium repens,* and *T. pratense*. Many clearings also contained dwellings, outbuildings, orchards, and gardens. Most homesteads were vacated by 1944, after the Queets River Corridor was added to ONP. Williams (1975) identified 43 clearings from former homesteads and provided crude vegetation maps and detailed cultural histories for six of the larger clearings.

Homesteads for my study are given in Table 2.1. Within these homesteads were fields on different alluvial terraces, which had different soil characteristics (Ch. 4). Consequently, each field is further designated with a letter that indicates height of alluvial terrace (L = low terrace, M = intermediate, or H = high). Experiments were conducted in homesteads #1 to 3. Homesteads with permanent plots include #4 and 5, while homesteads #6 to 8 represent fields used only in vegetation analysis. Selected fields included the six clearings (Table 2.1: #1, 2, 3, 5, 7, 8) detailed by Williams (1975). Field 6L was added because of its large size and accessibility, and the eastern part of Field 4H was added after noting a major invasion of *Picea* under conditions different from those in Fields 2M and 2H (absence of nurse logs, browner soils).

Locations, sizes, and years of homestead occupancy of the study fields are given in Table 2.1.

Queets River Valley

The Queets River has cut and filled a glacial outwash plain to create a 1 - 2.5 km wide valley floor, with 3 to 4 levels of alluvial terraces (Fonda 1974, Schroer et al. 1993). Soils of all study fields are alluvial. River erosion cut into some of the fields during the course of my study. Elevation of the fields range from 50 to 130 m a. s. l. The maritime climate is very wet and mild. Annual rainfall averages about 300 cm with most falling between October and May. Precipitation from June to August averages 24 cm. Precipitation and temperature records from the nearby Clearwater weather station during my study period are shown in Appendix 1.

In typical riparian succession in the western Olympic Mountains, *Alnus rubra* and *Salix* spp. colonize new alluvial surfaces. If undisturbed, *Alnus* will dominate, forming "alder flat" forests that persist for 80 to 100 years (Fonda 1974). *Alnus* stands are eventually replaced by *Picea sitchensis*. Over centuries (as indicated on higher terraces), *Tsuga heterophylla* increases in importance in the valley rain forests. Understories in the coniferous forests are dominated by *Polystichum munitum*, *Oxalis oregana*, and mosses. Understories in the alder flats include a number of exotic herbs, such as *Ranunculus repens* and *Poa trivialis*, which usually provide the majority of cover (Fonda 1974, DeFerrari & Naiman 1994). My study fields were bordered by *Picea* or *Alnus* forest, with a few areas bordered by recently cut river banks.

A large population of Roosevelt elk (*Cervus elephus roosevelti*) ranges through the valley, browsing heavily on shrubs and grazing in the fields (Schroer et al. 1993). Deer (*Odocoileus hemionus*) also occur, but are fewer in number; Leslie (1983) estimated deer biomass to be 7% that of elk. Exclosure studies in the Olympic rain forest indicated that cervid herbivory is important in structuring forest understory vegetation. Herbivory decreases shrub and fern cover and increases grass cover (Woodward et al.

1994, Schreiner et al. 1996). Elk numbers may have been higher during field abandonment in the 1930s and 1940s, but they have remained near their current levels since the 1950s (Woodward et al. 1994).

History of Invasion by *Carex obnupta, Cirsium arvense, Pteridium aquilinum,* and *Rubus laciniatus*

Five species (*Carex obnupta, Cirsium arvense, Pteridium aquilinum, Rubus laciniatus,* and *Picea sitchensis*) have invaded to dominate parts of the old fields, although the majority of cover remained dominated by pasture grasses and forbs (see Ch. 4). The first four species (non-trees) are reported here. *Picea* colonization is discussed in Ch. 3. Aerial photographs were the primary source of information to examine the invasion history. Photographs at a scale of 1:12000 were obtained from the Washington Department of Natural Resources, Olympia, for 1960 (Project WWJC-60), 1971 (OLY-71), 1981 (OL-81), 1990 (OL-90), and 1997 (OL-97). Photographs from 1939 were obtained from the National Archives, Washington, DC (GS-J). Cover changes were measured from scanned, magnified, and scaled images. Cover changes also were identified from color photographs from low-altitude flights in February 1975 (ONP files) and in July 1999. Additional sources include cover maps in Williams (1975) and matching surface photographs from 1975 and 1985 (ONP files).

Once established, all four species (*Carex obnupta, Cirsium arvense, Pteridium aquilinum,* and *Rubus laciniatus*) have the potential for aggressive, clonal expansion (Page 1986, Grime et al. 1988, Cooke et al. 1997). *Pteridium* and *Cirsium* tended to invade the study fields by frontal expansion from edges, while *Rubus* and *Carex* showed a pattern of nucleation (establishment at points within fields followed by expansion in diameter). Ability of *Rubus* to establish in the middle of fields may have been aided by dispersal by black bears (*Ursus americanus*), as berry-laden scat was noted.

Carex obnupta

Circular *Carex* patches first appeared on 1971 aerial photographs of Fields 2M, 3L, 3H, and 7L, but not until 1981 in Field 6L. Expansion rates of *Carex* edges were calculated from measurements of the DNR photographs. In three fields, mean *Carex* advance was 0.33-0.41 m/yr from 1971 to 1981, then slowed to 0.15-0.16 m/yr from 1981 to 1997. In Field 6L where *Carex* appeared later, mean expansion rate was 0.39 m/yr from 1981 to 1997, similar to the early rate in other fields. While some *Carex* populations were in low, wetter areas, many appeared and expanded within upland areas, especially in Field 3H.

Cirsium arvense

Cirsium has advanced steadily from east to west across Field 8H. It started as a small patch in 1939 but occupied three-quarters of the field by 1997. Mean rates of *Cirsium* advance along five reference lines were calculated for each interval between aerial photographs. This revealed a steady rate of *Cirsium* advance, which varied between 2.0 and 3.0 m/yr. Although *Cirsium* was present in parts of other fields (2L, 2M, 7L), its cover was usually lower than in 8H and its boundary not detectable on the photographs. In other fields (3L, 5L, 6L), *Cirsium* was present throughout meadows dominated by *Agrostis gigantea* (App. 3). However, *Cirsium* has not invaded areas of *Anthoxanthum odoratum* cover in 3H, 4H, and 7L (App. 3). *Anthoxanthum* has been associated with soils of low fertility (Grime et al. 1988), while *Cirsium* may require more favorable conditions (Klinka et al. 1989).

Pteridium aquilinum

Ability to detect *Pteridium* varied among images depending on photographic contrast and season of photography. Generally, *Pteridium* was already evident in most of the areas it now occupies in the earliest photographs in which it was detectable (usually 1960). The major exception to this was a southwest area of Field 3H (App. 3: Site 3H-PA), where *Pteridium* was not noted in 1975 in the low-flight aerials or on maps of Williams. In 1990, however, *Pteridium* covered most of the site (40-50 m out from forest edge). I noted that density of *Pteridium* plants varied greatly within a patch and that year-to-year patch boundaries were erratic (1996-1999). This pattern is consistent with studies of *Pteridium* stands in Great Britain that described cyclic succession in which *Pteridium* cover alternates with grassy cover (Watt 1947, Marrs & Hicks 1986). Marrs & Hicks (1986) also reported little increase in total area of presence of *Pteridium* between 1922 and 1984 on their sites, although there was great variability of *Pteridium* density over time within the area.

Rubus laciniatus

Few *Rubus* patches were apparent on the aerial photographs until 1971. Since 1971, *Rubus* patches have shown a continual increase in growth and numbers in parts of Fields 2L, 2M, 3L, and 7L. (The patches were numerous and very small on the photographs and not quantified.) Surface photographs of Field 7L revealed a dramatic increase in height, width, and number of *Rubus* patches between 1975 and 1985. However, in Field 6L, *Rubus* patches of 1975 have expanded, but establishment of new clones since 1975 was not evident. In Field 5L, the number of *Rubus* patches declined since 1975.

Table 2.1. Location, size, and years of homesteading of study fields.

In Field IDs: L = low terrace, M = intermediate terrace, H = high terrace.

Field ID	Williams number[1]	Latitude N	Longitude W	Area (ha) studied	Homestead years[2]	Local name[2]
1L	22	47°36'25"	124°02'55"	2.6	1890 - 1941	Kelly
1M	22	47°36'20"	124°02'55"	0.8	"	"
2L	21	47°35'50"	124°05'45"	3.7	1891 - 1944	Gwin
2M	21	47°35'45"	124°05'40"	7.5	"	"
2H	21	47°35'45"	124°05'30"	2.7	"	"
3L	20	47°35'00"	124°06'40"	2.2	1891 - 1925	Streater
3H	20	47°35'00"	124°06'48"	6.4	"	"
4H	19	47°35'16"	124°07'00"	4.2	([3])	
5L	23	47°36'40"	124°02'40"	3.9	1890s - ([3])	Barrington
6L	5	47°33'20"	124°13'00"	3.5	([3])	
7L	10	47°33'20"	124°11'15"	4.8	1890 - 1944	Higley
8H	34	47°38'10"	123°59'10"	5.8	1900s - 1944	Andrews

[1] Williams (1975), used by ONP;

[2] dates and names as described by Williams (1975)

[3] no data, but being farmed in 1939 aerial photographs

3. HISTORY AND DEMOGRAPHY OF TREE COLONIZATION

Introduction

The history of vegetation change is often inferred from chronosequences that substitute space for time (Pickett 1989). In studies of old field succession, spatial and temporal patterns of tree invasion are typically investigated only in the first few decades after abandonment (Myster 1993). In contrast, I was able to utilize a comprehensive aerial photographic record to examine 60 years of tree colonization of old fields in the Queets River Valley, Olympic National Park. I focused on spatial and temporal patterns of colonization and crown growth of invading trees.

In addition, I examined the demography and growth rates of tree saplings in three active areas of invasion by monitoring permanent plots. Although the primary inhibition of tree colonization of the Queets fields appears to involve failure of seedlings to emerge, the subsequent transition to mature trees of the few seedlings that do emerge may also be important. In particular, herbivory can have differential effects on the ability of tree species to colonize old fields (DeSteven 1991b, Hill et al. 1995, Lawson et al. 1999). *Tsuga heterophylla*, *Alnus rubra*, and *Frangula purshiana* are browsed by elk and deer in the Queets fields (Ch. 4). I wished to compare the growth and survival of saplings of these browsed species relative to the little-browsed *Picea sitchensis*.

The studies in this chapter are descriptive and exploratory, without *a priori* hypotheses. They provide fundamental information and generate insights on differential tree colonization of the fields. They also serve to place subsequent experimental studies into a broader framework.

Methods

Aerial photograph analysis

Aerial photographs of the Queets study fields (see Table 2.1 for field descriptions) at a scale of 1:12000 were obtained from the Washington Department of Natural Resources (DNR), Olympia, for 1960 (Project WWJC-60), 1971 (OLY-71), 1981 (OL-81), 1990 (OL-90), and 1997 (OL-97). Photographs from 1939 were obtained from the National Archives, Washington, DC (GS-J). Images were scanned and magnified to a scale of 1:2000. Individual canopy crowns of invading *Picea* trees were identified on the DNR photos. The threshold of crown visibility on these photographs is about 2 m in diameter. Crown widths of open-grown trees were measured on the scanned images. Crowns were considered open grown if > 50% of the crown was not in contact with other trees. Changes in tree cover also were examined on color photographs from low-altitude flights in February 1975 (Olympic National Park files) and in July 1999.

Permanent plots

Permanent plots (PP) were established along the edges of three fields early in 1998 to monitor tree sapling growth over two growing seasons. Individuals ranged from 3 to 450 cm in height, here referred to as saplings for convenience. Two of the locations (PP-2M & PP-4H) were chosen to represent active invasion of field edges by *Picea* and, to a lesser extent, *Tsuga* and *Frangula*. These areas were in field edges adjacent to two of three sites (Table 4.3) supporting mature *Picea* that invaded soon after field abandonment. Soils at PP-4H (in Site 4H-AO, see App. 3 for site soil and vegetation characteristics) were higher in organic matter and lighter in texture than those at PP-2M (in Site 2M-PA). Cover at PP-4H was dominated by *Pteridium* and *Anthoxanthum*; and cover at PP-2M by *Pteridium* and *Agrostis*. The third permanent plot (PP-5L) was established in Field 5L. This was located to include the most active area of *Alnus* invasion found in the fields.

Permanent plots contained quadrats that were 4 m wide along the forest edge and extended 20 m into the field. For PP-2M, thirty-five quadrats were established at random locations along a 350-m edge. For PP-4H, a contiguous array (44 x 20 m) of 11 quadrats was placed along the middle of a 60-m edge. PP-5L contained a contiguous array of 14 quadrats (56 x 20 m). Within a quadrat, all individuals were identified by a coordinate system to facilitate future relocation. Heights of saplings before the growing season were measured in 1998, 1999, and 2000. Leader growth began in May for most saplings. Evidence of browsing also was noted. The Queets fields were browsed by elk (*Cervus elephus roosevelti*) and to a lesser extent by deer (*Odocoileus hemionus*).

Data analysis

Relative growth rates (RGR) were used because they are the most appropriate measure of plant growth for comparative studies (Harper 1977, Zedaker et al. 1987). RGR was defined as one year's change in a growth parameter divided by the value of the parameter before the growing season. For example, if H_{1998} = height early in 1998 and H_{1999} = height early in 1999, % RGR in height for the 1998 season = $[(H_{1999} - H_{1998}) / H_{1998}] * 100$. Regressions of log RGR per year versus initial height were used to compare sapling growth on the permanent plots. For purposes of interspecies and interplot comparisons, I confined my analysis to open-grown saplings. Hence, I excluded from this analysis those few saplings with crowns that were beneath crowns of larger saplings. Saplings growing on nurse logs were also excluded, because these were limited to small areas within three quadrats in PP-2M and are unlikely to be representative.

To examine *Picea* crown diameter growth of trees on the aerial photographs, I used regressions of log RGR of crown diameter per year (averaged over the interval between photographs) versus diameter at the beginning of a photographic interval. For example, if D_{1981} = crown diameter in 1981 and D_{1991} = diameter in 1991, then % RGR = $100 * \{[(D_{1991} - D_{1981}) / 10] / D_{1981}\}$. Tests for coincidental regressions (Zar 1996) were used to compare growth rates between fields and between years in the permanent-plot data. The null hypothesis in the test for coincidental regression is that both the slopes and elevations of the regression lines are identical. In the photographic analysis, there were too few data to compare differences in RGR among decades.

Results

Aerial photographic history

For each of 11 fields (Table 2.1), I studied eight aerial photographs (1939, 1960, 1971, 1975, 1981, 1990, 1997, 1999). Trees have not invaded across most 1939 field boundaries. However, in some areas, the photographs revealed two patterns of tree colonization, which I term "area filling" and "edge advance". Parts of six fields (Table 3.1) demonstrated "area filling" (colonized by simultaneous invasion of an entire area, including jump dispersal). Since 1971, parts of seven fields (Table 3.2) exhibited "edge advance" (progressive advancement of trees from the forest edge, or diffusion).

From 1939 to 1971, six areas were colonized by area filling (Table 3.1). These areas extended up to 150 m from the 1939 forest edge. Area filling is illustrated in Fig. 3.1 (1971 photograph of Site 2M-PS). (Although new trees have continued to fill these areas after 1971, most *Picea* tree invasion during 1971-1997 was by "edge advance".) Two of the areas invaded before 1971 were on low-terrace fields, which was notable because *Picea* sapling invasion on low terraces was virtually absent in 1998 (Table 4.5). One of these low fields (2L) was invaded by 37 trees before 1971, but exhibited no further invasion by edge advance after 1971. Scattered logs were evident in early photographs of two areas (in Fields 2M & 2H). Otherwise, there were no noticeable differences in the 1939 photographs between the invaded areas and adjacent areas that had not been invaded. However, all six of these invaded areas showed evidence of *Pteridium aquilinum* cover in later aerial photographs.

Edge advance since 1971 has occurred at low rates in limited parts of a few fields (Table 3.2). Edge advance is illustrated in Fig. 3.2 (1997 photograph of Site 3H).

Fields 3H & 4H have shown a higher rate of edge expansion than others (Table 3.2). These two fields also showed earlier colonization by trees prior to 1971 than did other areas (Table 3.1). The areas of *Picea* tree advance, as shown by the photographic data (Table 3.2) are generally the same as areas of *Picea* sapling advance in a 1998 edge survey (Ch. 4). However, the number and distribution of saplings found in active edges in 1998 was high in relation to the tree invasion rate shown on the 1971-1997 photographs. These areas of intense edge invasion may be a recent phenomenon. Saplings in these areas were visible in the 1999 low-altitude color photographs, but similar areas were not seen in the low-altitude 1975 photographs. There was no evidence on the aerial photographs of appreciable areas of invasion of tree species other than *Picea*.

Demography and growth of saplings in permanent plots

Picea saplings in the two permanent plots exhibited little mortality through the two growing seasons (Table 3.3). Almost all saplings increased in height annually. (*Picea* sapling ages ranged from 1 to ~15 yr, the upper limit based on cores of larger saplings). RGR declined with height, as expected for conifers (Zedaker et al. 1987).

Regressions of log RGR with heights at the beginning of the growing season of four cases (PP-4H: 1998, 1999 and PP-2M: 1998, 1999) were each significant at $P < 0.0001$, although there was wide variation in growth rates among smaller saplings (Fig. 3.3). This growth pattern did not change for saplings > 1 m that overtopped adjacent cover. Tests for coincidental regressions (in both slopes and elevations) revealed greater differences between years than between fields (Table 3.4). Growth rates were lower in 1999 than in 1998. Temperatures in 1999 during May and June were lower than 1998 (App.1).

Mortality was much higher on smaller saplings of *Tsuga* than on *Picea* (Table 3.3). Patterns of *Tsuga* RGRs were highly variable among fields and years. Many plants decreased in height. Signs of browsing on *Tsuga* were abundant. Differences in growth patterns between *Picea* and *Tsuga* are illustrated by Fig. 3.3 of 1999 relative height growth of the two species in PP-2M.

In January 2000, there were only three *Tsuga* saplings > 1 m tall in the permanent plots compared to 130 *Picea* saplings. Only one *Tsuga* sapling grew above the browse line (about 2 m above ground). It increased from 3.1 to 4.5 m in height in 2 years. Ages estimated by annual growth rings of three *Tsuga* saplings that were between 40 and 62 cm in height were 16-17 yr.

Alnus and *Frangula* showed patterns similar to *Tsuga*, with variability in RGR and difficulty in growing above the browse line (Table 3.3). *Alnus* and *Frangula* exhibited bushy growth, as branch terminals were browsed back. Crowns of heavily-browsed *Tsuga* saplings, however, were cylindrical in shape with foliage close to a thick central stem.

Demography and growth of open-grown Picea trees from aerial photographs

From the analysis of *Picea* crown growth from 1960 to 1997, RGRs of crown widths decreased logarithmically with initial width. No significant difference in growth rates was found between trees in the low-terrace Field 2L and the high-terrace Field 3H (Fig. 3.4). Regressions of RGR with log diameter of the crown were significant at $P < 0.0001$ for both fields, with the two regressions coincidental ($F_{2,98} = 2.2$, $P > 0.10$, equation: % RGR per year in crown diameter = 32 - 29 * log initial diameter). No mortality was noted among these trees ($n = 70$), except for a few trees lost to river erosion.

DISCUSSION

Most field edges showed no tree invasion since abandonment. Where *Picea* invasion occurred, two patterns were observed: filling of an area by trees soon after field abandonment and a more recent, slower advance from forest edges. Tree colonization of old fields usually is concentrated at the edge (Myster 1993, Hill et al. 1995, Pinder et al. 1995, Lawson et al. 1999), but broader invasion of fields by species with light, wind-dispersed seeds also has been reported (Myster 1993). The ability to invade areas such as Field 2M (Fig. 3.1) indicated that *Picea* colonization is not limited by seed dispersal. *Tsuga* seedlings also were able to invade a permanent plot (PP-4H) that is over 100 m from mature trees. Harris (1967) noted that *Picea* and *Tsuga* regenerated from seed dispersal throughout a 1600- x 1600-m clearcut in Alaska. It is unlikely that lack of colonization of the Queets fields by *Picea*, *Tsuga*, or *Alnus* (also small, wind-dispersed seeds) can be attributed to seed dispersal limitation.

Except for two areas with nurse logs, I could not detect differences in the aerial photographs between areas that were colonized by *Picea* and adjacent areas that were not. Whether or not fields have been plowed prior to abandonment has been implicated in differential woody invasion in other studies (Motzkin et al. 1996, Stover & Marks 1998). The invaded areas on the Queets fields that contained scattered logs were unlikely to have been plowed. However, the plowing status of other invaded areas was unknown, since evidence of plowing was not discernible on the photographs (or in the young alluvial soils, which lacked horizons). The presence of *Pteridium* in the photographs in all six locations that were invaded prior to 1971 suggests an association between *Pteridium* and *Picea* invasion.

In contrast to my findings that *Picea* currently has difficulty invading low-terrace fields, the aerial photographs revealed that *Picea* did invade two areas on low terraces in the decades immediately after abandonment. Perhaps an "invasion window" for colonization (van der Valk 1992) has closed. The field edges of these areas now show no *Picea* seedling invasion. They are now dominated by *Pteridium* in association with the sodgrass *Agrostis*. Perhaps growth of *Agrostis* since abandonment closed the invasion window (or, alternatively, an *Agrostis* boundary may have existed at the time of abandonment).

Why were some areas that are now being colonized by edge advance not invaded by *Picea* earlier? The recent advance was confined primarily to edges dominated by

Anthoxanthum odoratum or *Pteridium*. Perhaps effects of the forest on the edge, such as microclimate amelioration (Cadenasso et al. 1997) or increased input of organic matter to field soil, have made these cover types invasible over time. These edge processes may not yet be enough to overcome inhibition in other vegetation types, such as that dominated by *Agrostis*.

Once tree seedlings emerged in the Queets fields, mortality rates were low. This supports my observation that the primary barrier to tree colonization is seedling establishment. Most *Picea* saplings survived each year and increased steadily in height. In contrast to results of Hill et al. (1995), the growth rates of *Picea* saplings did not exhibit suppression when growing below surrounding *Pteridium* or grass cover. There was no increase in growth rate when the saplings overtopped adjacent cover.

In contrast to *Picea*, the ability of *Tsuga*, *Alnus*, or *Frangula* to invade the fields appeared to be substantially decreased by herbivory. Growth rates in the permanent plots were erratic and sometimes negative. The importance of cervid herbivory in the differential success of tree species in old fields has been documented by DeSteven (1991b), Hill et al. (1995), and Lawson et al. (1999). In their studies, as in mine, herbivory primarily resulted in the continual reduction of new growth rather than direct mortality. However, this causes saplings to spend many years below the browse line, increasing the cumulative probability of mortality. (I caution that my study only encompassed two years and may not have captured extreme herbivory events.) In the surrounding temperate rain forests, elk herbivory is known to depress *Tsuga* regeneration in favor of *Picea* (Franklin & Dyrness 1973; Woodward et al. 1994).

Picea saplings that emerge in the Queets fields experience little mortality and steady growth rates. If land managers wish to accelerate the very slow succession of this system, perhaps the emergence barrier to colonization can be overcome by transplanting *Picea* saplings. However, I further caution that *Picea* sapling demography was measured for only two years in edge plots that were not dominated by *Agrostis*. In my experimental studies (Ch. 6), transplanted *Picea* saplings grew more slowly in *Agrostis* than in *Pteridium*.

Natural reforestation of the Queets fields by *Picea* may take several centuries. Present active invasion by saplings is limited to bands less than 10 m wide adjacent to mature trees. Furthermore, along most edges, there is no current seedling invasion. Of course, colonization dynamics may be altered over time by changes in field cover (Ch. 2) and soil development. Substantial colonization by *Tsuga*, *Alnus*, and *Frangula* is even less likely, since their current invasion is also limited to narrow edges where they are strongly suppressed by herbivory.

Table 3.1. Invasion of parts of six fields by *Picea sitchensis* by area filling prior to 1971; first appearance of trees on 1:12000 aerial photographs.

	soil terrace type[1]	# trees first appearance 1960	 1971	maximum distance in m to 1939 forest edge
sites sampled in 1997[2]				
2M-PS[3]	high	27	82	150
2H-PS	high	11	36	70
4H-PS	high	60	37	90
other areas[4]				
1L	low	1	3	8
2L	low	12	25	80
3H	high	16	11	30

[1] types described in Ch. 3; [2] sites described in Ch. 3 & App. 3; [3] may include a few *Tsuga heterophylla* trees; [4] identified by invaded field; not included in 1997 field survey

Table 3.2. Invasion of old fields by *Picea sitchensis* by edge advance since 1971; first appearance of trees on 1:12000 aerial photographs. All study fields included.

	# trees first appearance			maximum distance in m
Field	1981	1990	1997	to 1971 forest edge
high terraces[1]				
2M	5	1	3	25
2H	2	3	3	30
3H	2	20	5	15
4H	2	1	10	12
8H	0	0	0	-
low terraces[1]				
1L	1	0	0	15
2L	0	0	0	-
3L	2	1	3	6
5L	0	0	0	-
6L	0	0	0	-
7L	0	4	1	60[2]

[1] terrace soils described in Ch. 3; [2] trees in 7L invaded as scattered isolates in fields rather than near edge

Table 3.3. Mortality and relative growth rate (RGR) in height by size class of tree seedlings in permanent plots, 1998-2000. *Picea*, *Tsuga*, and *Frangula* in plots PP-2M & PP-4H. *Alnus* in PP-5L. Size class distribution is underlined and in bold.

	1998 growing season				1999 growing season				2000
height in cm	**n**^{1}	% die^2	mean %RGR	s.d.^{3} RGR	**n**^{1}	% die^2	mean %RGR	s.d.^{3} RGR	**n**^{1}
Picea sitchensis									
1 - 10	**106**	4	76	± 53	**57**	11	68	± 59	**41**
11 - 25	**131**	2	57	± 31	**165**	2	35	± 29	**149**
26 - 50	**50**	0	56	± 27	**94**	0	35	± 21	**112**
51 - 100	**56**	0	42	± 16	**48**	0	36	± 14	**65**
101 - 200	**64**	2	37	± 12	**76**	0	27	± 18	**68**
201 - 450	**15**	0	33	± 9	**33**	0	20	± 14	**62**
Tsuga heterophylla									
1 - 10	**14**	50	57	± 50	**8**	25	30	± 43	**11**
11 - 25	**16**	19	31	± 24	**19**	5	10	± 37	**16**
26 - 50	**14**	0	14	± 26	**24**	4	22	± 34	**24**
51 - 100	**6**	0	- 9	± 22	**11**	0	18	± 25	**16**
101 - 200	**1**	0	24	-	**1**	0	19	-	**3**
201 - 450	**0**				**0**				**0**
Alnus rubra									
1 - 10	**1**	0	210	-	**0**				**0**
11 - 25	**8**	0	79	± 32	**3**	0	116	±116	**5**
26 - 50	**18**	0	41	± 22	**18**	17	- 5	± 27	**15**
51 - 100	**27**	0	20	± 22	**32**	6	- 1	± 15	**28**
101 - 200	**6**	0	9	± 11	**10**	0	14	± 14	**12**
201 - 450	**0**				**0**				**0**

Table 3.3. (continued)

	1998 growing season				1999 growing season				2000
height in cm	n[1]	% die[2]	mean% RGR	s.d.[3] RGR	n[1]	% die[2]	mean %RGR	s.d[3] RGR	n[1]
Frangula purshiana									
1 - 10	1	0	225		1	0	75		4
11 - 25	6	0	31	± 33	11	20	- 22	± 38	9
26 - 50	10	0	29	± 39	17	12	2	± 43	19
51 - 100	14	0	15	± 13	19	0	- 2	± 28	21
101 - 200	14	0	11	± 25	18	0	9	± 21	18
201 - 450	3	0	8	± 10	3	0	4	± 11	7

[1]n = number at beginning of growing season; [2]annual rate, measured each year before growing season; [3]s. d. = standard deviation

Table 3.4. Tests for coincidental regressions of RGR with log initial height of *Picea* among two permanent-quadrat locations and two growing seasons. 1999 coincidental regression: RGR per yr in height (%) = 67 - 19 * log (inital height).

test pairs	F	df[1]	df[2]	P[3]
1998: PP-2M vs. PP-4H	4.85	2	414	0.008
1999: PP-2M vs. PP-4H	1.14	2	461	> 0.25
PP-2M: 1998 vs. 1999	20.24	2	417	< 0.0005
PP-4H: 1998 vs. 1999	13.02	2	458	< 0.0005

[1] df of numerator; [2] df of denominator; [3] Probability that regressions are coincidental (both slopes and elevations)

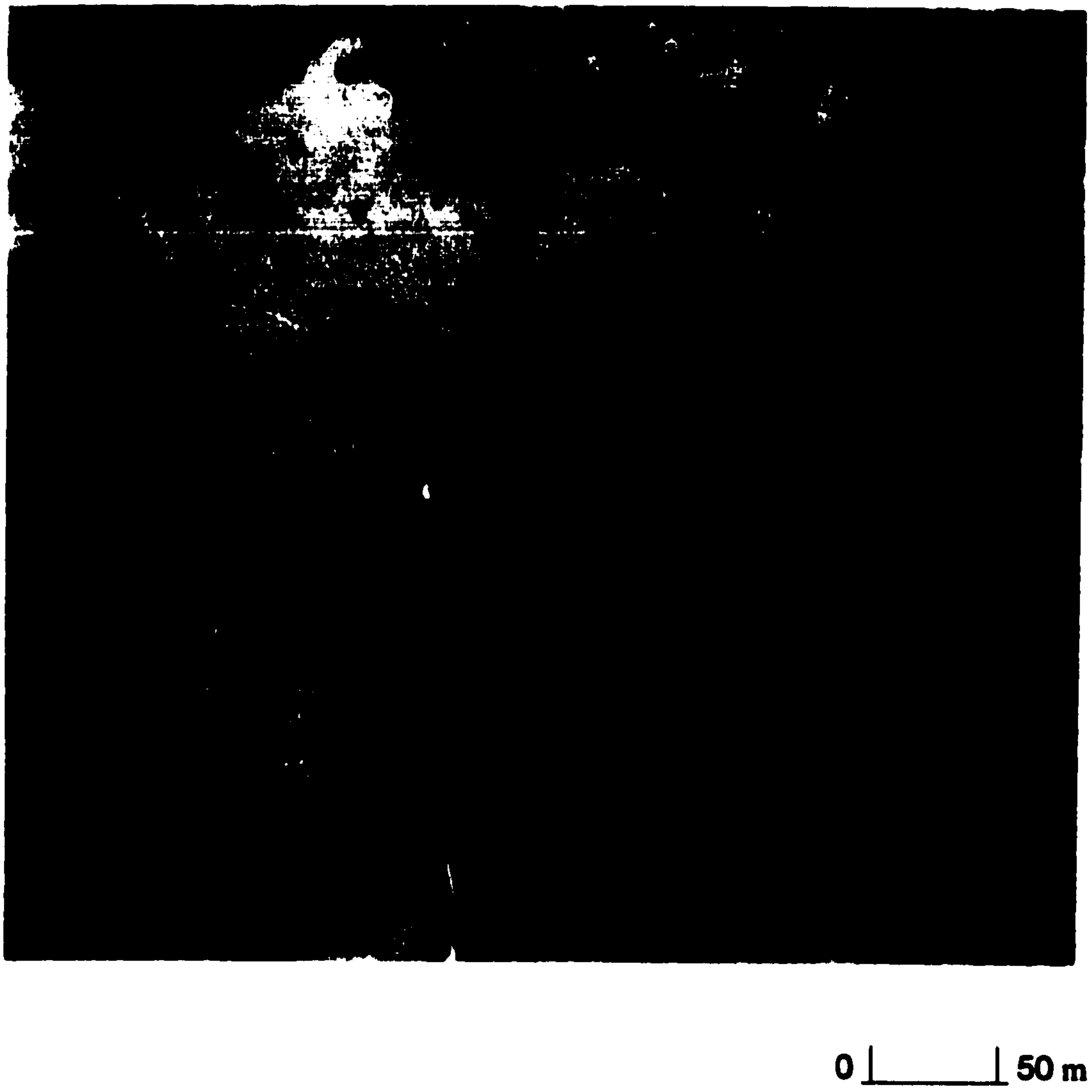

Figure 3.1. Aerial photograph of Site 2M-PS in 1971 illustrating area filling by *Picea* (with occasional *Tsuga*; *Tsuga* cover was ~5% that of *Picea* cover in 1997). Mature *Picea-Tsuga* forest is at the top. Lighter cover in Site 2M-PS is probably *Pteridium*. Some scattered logs are visible as white lines. Field 2L is in lower right, separated from 2M by a stream with a strip of young *Alnus*.

Figure 3.2. Aerial photograph of Site 3H-PA in 1997 illustrating edge advance by *Picea*. Mature *Picea-Tsuga* forest is at the top and left. Isolated *Picea* in lower left center first appeared in 1971 photograph. Smaller crowns along edge are *Picea* that appeared in 1981-1997 photographs. Light gray patches in lower right are *Carex obnupta*.

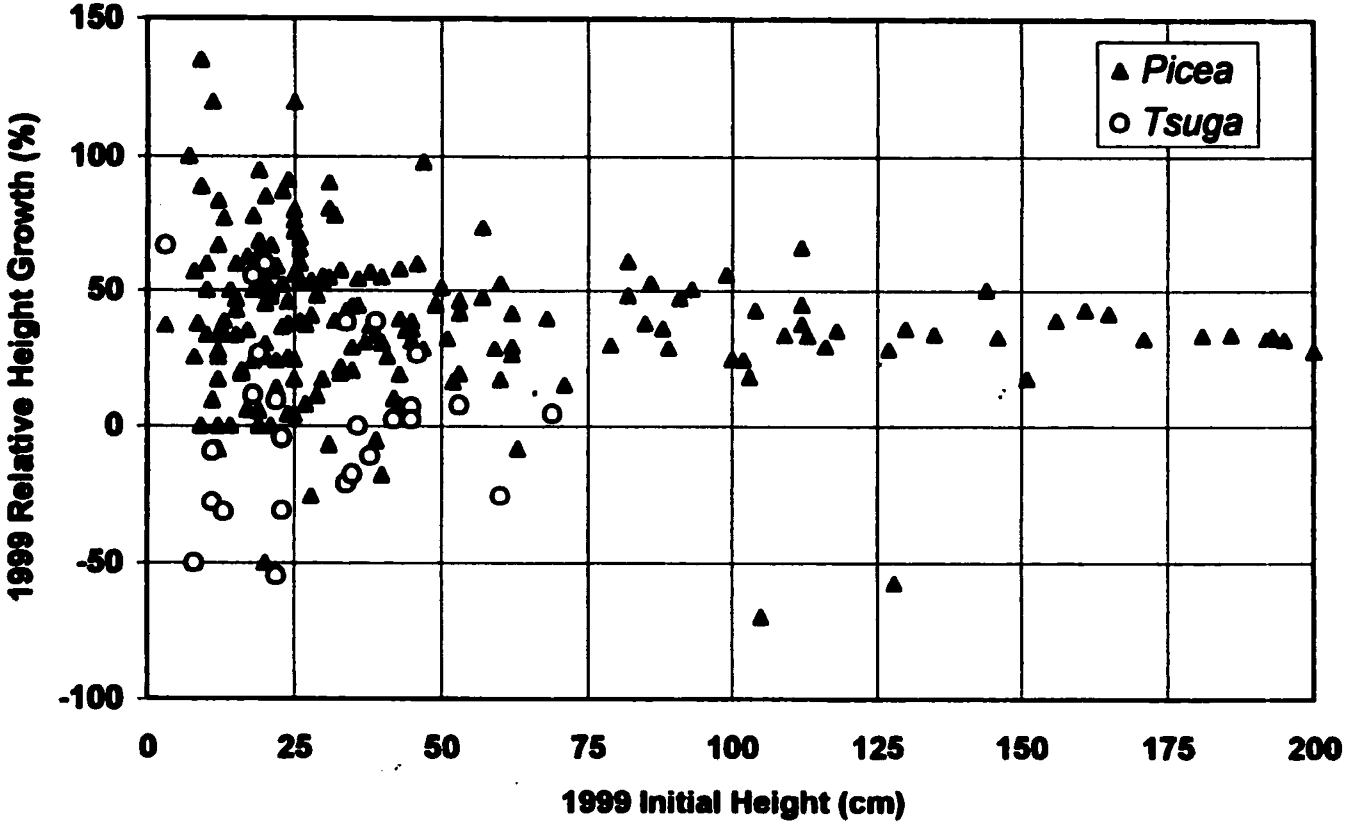

Figure 3.3. 1999 relative growth rate (RGR) in height of *Picea* and *Tsuga* saplings in permanent quadrats in Field 2M. Pattern of *Picea* growth continued with saplings > 200 cm (not shown).

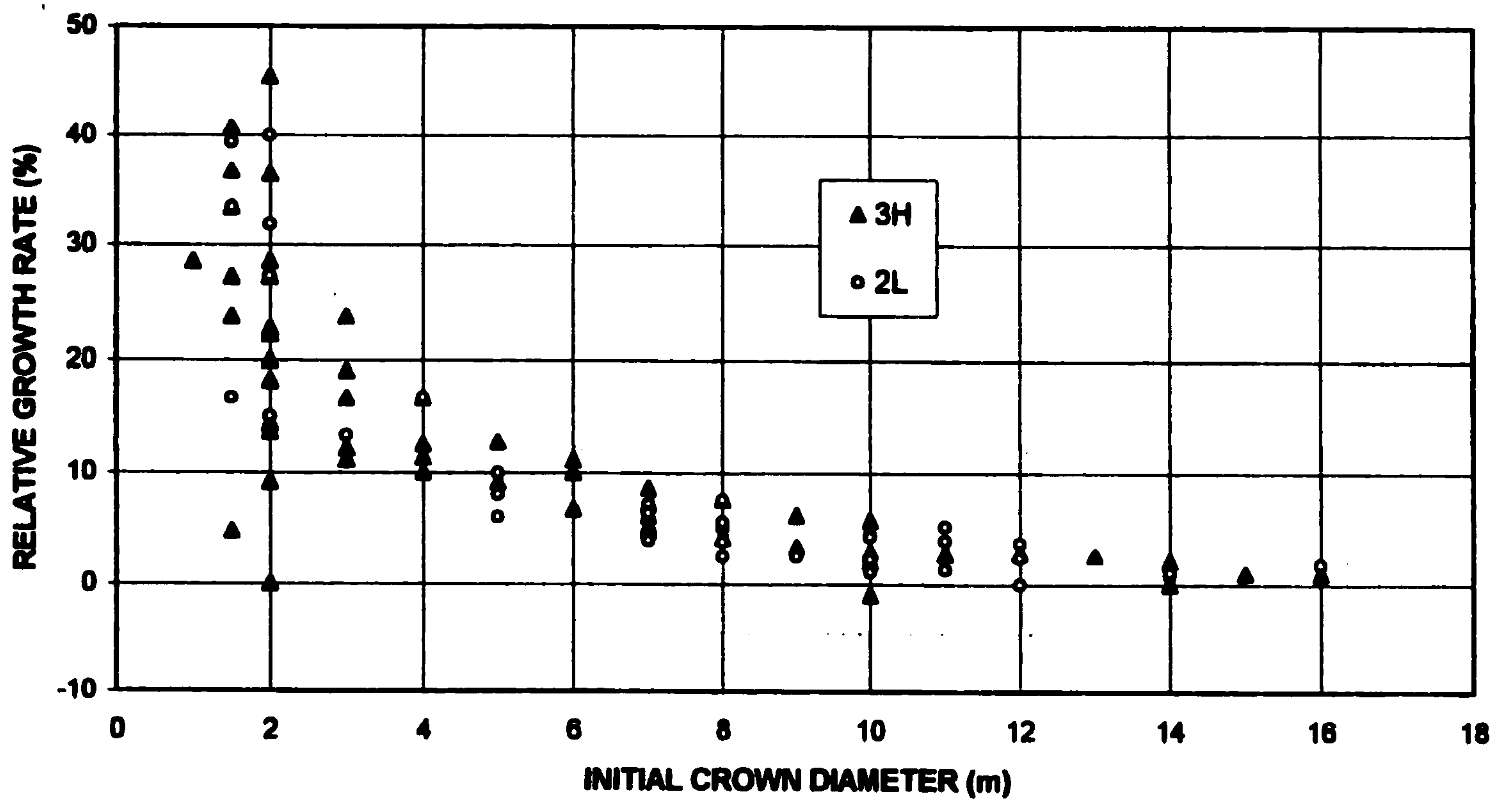

Figure 3.4. Relative Growth Rate (RGR) of crown diameter per year of open-grown *Picea* vs. diameter at the beginning of an aerial-photograph interval for a low terrace (2L) and high-terrace (3H) field. Regressions of RGR vs. log initial diameter were coincidental for the two fields.

4. INSIGHTS FROM VEGETATION ANALYSIS

Introduction

Old field succession in temperate forests is typically rapid (Keever 1983; Falinska 1991; Myster 1993; Smit & Olff 1998). Woody plants normally invade within a decade and dominate within 20 to 40 years. In contrast, most old fields abandoned six decades ago within a temperate rain forest in the Queets River Valley of Olympic National Park (ONP), Washington, USA show little invasion by trees. Lack of tree invasion of old fields of similar age has been reported elsewhere (Osbornova et al. 1990; Inouye et al. 1994; Prach et al. 1996), but usually under stressful conditions. The Queets fields occur on fertile soil in a moderate climate that can support lush forests.

Tree establishment can be inhibited by competition from herbs (DeSteven 1991b; Gill & Marks 1991; Berkowitz et al. 1995) or by herbivory (DeSteven 1991b, Inouye et al. 1994). Some shrubs (Werner & Harbeck 1982) and herbs (Gill & Marks 1991) may also facilitate tree colonization. Land-use history, whether fields had been cultivated or pastured, can affect tree invasion as well (Motzkin et al. 1996; Stover & Marks 1998).

While invading trees are absent from most of the Queets fields, parts of some fields are being invaded by *Picea sitchensis*. The differential rates of succession among the fields and the generally slow succession led me to ask: what factors influence tree establishment in the Queets fields?

This chapter reports the results of two vegetation analyses of the Queets fields. A 1997 field survey was designed to describe the vegetation of the fields and to generate hypotheses about how tree colonization is related to vegetation, soils, and land-use history. The field survey data were analyzed by cluster analysis, indirect ordination, and direct ordination. This was followed by a 1998 survey of sapling invasion of the edges of fields. The edge survey was designed primarily to examine hypotheses generated by the field survey.

Study Area

The study areas were eleven abandoned fields arrayed along 15 km of the Queets River within ONP (Table 2.1). These were homesteaded beginning in 1890 (Williams 1975). The fields were used for pasture, hay, or oat crops. Most homesteads were abandoned by 1944 after the Queets River Corridor was added to ONP. Williams (1975) located 43 fields and provided histories and maps for nine of the eleven that I studied. Field sizes ranged from 2.5 to 8.5 ha. The Queets River has formed a 1 to 2.5 km wide valley floor on a glacial outwash plain, with three or four alluvial terraces. Primary succession on fresh alluvium leads to a forest dominated by *Alnus rubra* on the lowest terrace, which is replaced by *Picea sitchensis* and *Tsuga heterophylla* on older terraces (Fonda 1974). Mean annual precipitation is about 300 cm, mostly falling as rain between October and May. Rainfall from June to August averages 24 cm (App. 1). Temperatures are mild, with 1°C average minimum in January and 24°C average maximum in August (NOAA, 1996-1999).

A large Roosevelt elk population (*Cervus elephus roosevelti*) resides in the valley (Schroer et al. 1993), browsing heavily on shrubs and grazing the fields. Deer (*Odocoileus hemionus*) occur in much lower numbers (Woodward et al. 1994). Exclosures in the Olympic rain forest have shown that cervid browsing helps to shape understory vegetation, by decreasing shrub and fern cover and increasing grass cover (Schreiner et al. 1996).

Field Survey

Methods

Fields were sampled along a grid of lines 25 m apart (Fig. 4.1) during June-July 1997. Sample points were determined in a stratified random manner (set at random distances between 0 to 9 m from grid intersections). At each point, percent cover of each vascular plant species was determined in nested quadrats of 1-m^2 (all species), 4-m^2 (shrubs and ferns only) and 100 m^2 (trees only). Diameters of any trees were measured at 1.25-m height. Saplings (0.5 - 5 m tall) were counted. A total of 502 sets of nested quadrats (23-88 per field) were sampled. The layout and terminology for the sampling scheme are illustrated in Fig. 4.1. Plant nomenclature follows Kartesz (1994).

Soil samples were collected from 136 of the quadrats (every fourth quadrat) by a hand trowel at 5 to 20 cm depth. In the laboratory, soils were air dried, rolled and passed through a 2-mm sieve. Soil particle size was determined by the hydrometer method (Bouyoucos 1951). Soil pH was determined from a 1:1 dry soil to water mixture. After the fields were partitioned into 23 sites for CCA analysis (see below), three soil samples were collected from each site within two days during the dry summer for measurements of soil moisture and organic matter. Soils were oven-dried at 105°C for gravimetric water content and combusted in a muffle furnace at 450°C for organic matter content (Wilde et al. 1972).

For vegetation analysis, I first classified the 502 quadrats using Ward's agglomerative method (McCune & Mefford 1997). Tree cover data from 1-m^2 quadrats (rather than 100-m^2 plots) were used for cluster analysis because they derive from a similar spatial scale as the herb and shrub data. Species with fewer than five occurrences were deleted, leaving 40 species in the analysis. Detrended Correspondence Analysis (DCA) was used on the same data set, with rare species downweighted (McCune & Mefford 1997).

Canonical Correspondence Analysis (CCA) was used to relate the environmental variable matrix to the vegetation matrix. To conduct this analysis, fields with major cover transitions were partitioned into two or three sites each, for a total of 23 sites in the 11 fields. Species with fewer than three occurrences were deleted, leaving 42 species. The species matrix consisted of mean cover of all quadrats within a site. The environmental matrix included median values of soil pH, moisture, organic matter and texture (as percent sand). Medians were considered to be a more appropriate measure of central tendency since sites were limited to three samples for soil moisture and organic matter. Sand percentage (that is, separating particle size into sand and fine soils) was the only texture value used because (1) growth of plants in heavier soils may be influenced more by soil structure than by fractions of silt versus clay (Wilde et al. 1972), (2) clay content was low (1.5 – 14.0 %), and (3) further separation into clay and silt had little effect on preliminary ordinations. Two land-use history variables were included. Agricultural use intensity (AI) on the fields prior to abandonment was indexed (as a quantitative variable) from 1939 aerial photographs and historical records as: 1 = pasture with scattered logs left in field, 2 = pasture in 1939, 3 = crops (hay or row crops) in 1939. A burning variable (BURN) was indexed as: 1 = neither charcoal in soil nor historical records of burning, 2 = some charcoal in soil samples, 3 = abundant charcoal in soil samples and historical records of burning. Forward selection of environmental variables (ter Braak & Smilauer 1998) was used to determine which environmental variables contributed most to explanation of variance. Monte Carlo permutation tests were used to see if observed patterns differed from a random relationship.

McCune & Mefford (1997) caution that the significance of the interset correlations of environmental variables with CCA axes is problematic, because the ordination axes were constrained by these environmental variables. (Thus, the interset correlations will be higher than for an unconstrained ordination.) Therefore, I also ran a separate DCA of the 23 sites and examined the significance between the environmental variables and axes scores of the sites by Spearman rank correlations.

Results

Cluster Analysis. Cluster analysis produced seven cover types (Table 4.1). Two exotic pasture grasses dominated the majority of quadrats: the *Agrostis gigantea* cover type occupied 45% of the quadrats, and the *Anthoxanthum odoratum* cover type dominated 12%. Other cover types were dominated by species that have colonized since the fields were abandoned: *Carex obnupta* (native, 5% of the quadrats), *Cirsium* *arvense* (exotic, 9%), *Pteridium aquilinum* (native, 13%), *Rubus laciniatus* (exotic, 8%) and *Picea sitchensis* (native, 8%).

Vegetation within cover types among the 11 fields was similar in composition (App. 3). The *Agrostis* cover type was present in all 11 fields. Other cover types were present in 4-7 fields (Table 4.1). Native understory species that are common in the surrounding forests were rare in the fields and were associated with *Picea* or *Pteridium* invasion (Table 4.1). All species encountered in the 1997 field survey are listed in Appendix 2.

Indirect ordination. Detrended Correspondence Analysis (DCA) of the 502 quadrats was used to examine relationships of *Picea* to other cover types. Therefore, quadrats are grouped by cover type for this analysis (Fig. 4.2), and not grouped by field. Figure 4.3 illustrates that field groups are widely overlapping. This is because cover patches of vegetation differ within fields but cover types are similar among fields (Table 4.1, App. 3). Fields with many patches, such as 2M and 3H, range throughout the ordination (Fig. 4.3).

The first eigenvalue of the DCA accounted for 20% of the variance and the second eigenvalue, 11%. These values are typical for DCA analysis with this many species. DCA revealed an elongated array of quadrats dominated by *Agrostis* and *Anthoxanthum* (Fig. 4.2). Quadrats that were dominated by the five major invading species scattered outward from the grass-dominated array. This pattern may suggest directions of successional change from the pasture vegetation assumed to be present upon abandonment (1939 aerial photographs show no evidence of the five invading species in the fields, see Chs. 2 & 3). Quadrats dominated by *Picea* had high values on Axis 1. Increasing values along Axis 1 also showed a trend in cover type from *Anthoxanthum* to *Pteridium* to *Picea* (Fig. 4.2). Quadrats dominated by *Cirsium*, *Carex*, or *Rubus* do not show association with *Picea* quadrats. *Picea* was not present in quadrats of these cover types (Table 4.1).

Species ordination scores of the first two axes of DCA are presented for the common species in Table 4.2. *Picea* had the highest DCA-1 value among these species. As expected, the species ordination pattern of the seven dominant species in Table 4.2 is similar to the pattern displayed by their cover types in the site ordination of Fig. 4.2. Table 4.2 also shows ordination scores of the subdominant species in relation to those of the dominants.

Direct ordination. Canonical Correspondence Analysis (CCA) of the 23 sites provided insight into factors associated with the vegetation patterns. The first three eigenvalues account for 42% of the variance in the species data. CCA-1 accounts for 28 % of variation in species data and 58% of variance of the species-environment relationship. The Pearson species-environment correlation is 0.91 for CCA-1 and 0.86 for CCA-2. Monte Carlo tests (200 permutations) showed that CCA-1 was significant at $P = 0.005$ and CCA-2 at $P = 0.025$.

The significance of CCA interset correlations of environmental variables with the first two axes was supported by Spearman rank correlations of environmental variables with DCA axis scores for the 23 sites (Table 4.3). Relationship of environmental variables to species dominants is illustrated in the biplot in Figure 4.4. In the biplot, the longer the environmental vector the stronger the relationship with the ordination. Species relationships to environmental variables can be pictured by running a perpendicular from the species location (centroid) to the vector (imagine the vector as extending through the entire ordination). Species with perpendiculars closer to the head of the arrow show a stronger relationship to the variable.

CCA-1 was negatively associated with the intensity of agricultural disturbance (AI) and positively associated with burning prior to clearing (Fig. 4.4). All soil variables except texture (% sand) were strongly correlated to CCA-1. The trends in soil values suggested a "soil age" gradient (Fonda 1974). Higher terraces generally have higher values on CCA-1. As the parent material aged, soil organic matter (range: 2.3 to 11.2%) and moisture (range: 26 to 47%) increased while soil pH (range: 4.0 to 4.6) decreased. Forward selection of environmental variables identified agriculture intensity (P = 0.005 in Monte-Carlo permutations) and soil pH (P = 0.01) as the environmental variables most strongly related to CCA-1. CCA-2 shows association with soil texture (range from 35 to 72% sand). Values of environmental variables and major species cover are listed for the 23 sites in Appendix 3.

The distribution of the seven dominant species on the CCA of 23 sites (Fig. 4.4) was similar to their distribution in the DCA of 502 quadrats (Fig. 4.2). This indicated that CCA retained the pattern determined by vegetation alone, while providing environmental explanations of this pattern. *Picea* cover showed a strong positive association with CCA-1.

Exploratory analysis by CCA suggested the following hypotheses about colonization by *Picea*: Invasion is more likely in fields that (1) were less disturbed by past agricultural use and in which logs had been left; (2) have older soils with higher organic matter, moisture and acidity; and (3) were burned before clearing. The combined results of CCA and DCA suggest the following hypotheses about relationships among major species : (1) *Pteridium* may facilitate *Picea* invasion and (2) *Cirsium*, *Carex* and *Rubus* patches represent successional pathways that do not lead to *Picea*.

Picea-dominated sites. Three of the 23 sites were substantially invaded by *Picea sitchensis* after field abandonment and now contain mature trees. Some characteristics of *Picea* on these sites are presented in Table 4.4. About half of the *Picea* trees were found on nurse logs in two sites, but logs were not evident in the third. Saplings also were abundant at these sites, indicating that *Picea* will likely continue to expand in these sites.

Edge Survey

Introduction

Most *Picea* cover in the 1997 field survey were trees that colonized soon after abandonment (Ch. 3). I observed that *Picea* seedlings and saplings were also invading the edges of some fields at varying density (ages ~ 1 – 15 yr, see Ch. 3). I designed the 1998 edge survey to explore this differential sapling establishment to examine hypotheses concerning *Picea* colonization generated by the 1997 vegetation analysis. Thus, hypotheses were generated by data on historic *Picea* tree invasion, but are tested with data on recent *Picea* sapling invasion. The edge survey also examines sapling establishment of species other than *Picea*, without *a priori* hypotheses.

Picea sapling invasion was hypothesized to be positively correlated with *Pteridium* and *Anthoxanthum* cover types and negatively associated with *Agrostis*, *Carex*, *Cirsium*, and *Rubus* cover types. *Picea* invasion was hypothesized to be positively correlated with soil moisture, soil organic matter, and past burning and negatively correlated with soil pH and intensity of past agricultural use.

Methods

During August-September 1998, I sampled a total of 274 plots (10-36 per field), which were located every 25 m along the forest-field edge (defined as vertical plane of the edge of continuous forest canopy) in the 11 fields sampled in the 1997 field survey. Plots were 10 x 20 m and placed with the long axis perpendicular to the edge (Fig. 4.1). The survey followed the present forest border of the three sites in the 1997 field survey that are now dominated by mature *Picea*. This allowed examination of recent sapling invasion at these edges. For each plot, I determined the percent cover of six cover types (*Agrostis, Anthoxanthum, Carex, Cirsium, Pteridium, Rubus*) previously defined by cluster analysis of the 1997 data. As patches of cover types are coarse-grained, partitioning a 10 x 20 plot into cover types was readily accomplished. The number of hectares sampled for each category of cover and soil type is listed in Table 4.5.

In each plot I measured all saplings between 50 and 500 cm in height and their distance from the edge. For each sapling I noted immediate surrounding cover type and signs of browsing. Only saplings ≥ 50 cm were included (1) to ensure that only plants that have successfully established beyond the small seedling stage were sampled and (2) to tally saplings in edges of all fields in a time-efficient manner in late-summer cover. Ages of *Picea* saplings of 50-500 cm are estimated to range from 6 to 15 yr, based on growth rates in my permanent quadrat studies (Ch. 3). For each plot, I also recorded the species identity of the five trees with the tallest crowns in the adjacent forest canopy.

The hypotheses were tested by Spearman rank correlations between density of sapling invasion and measurements of cover type, soil, and land-use history. Each rank correlation was considered as a separate hypothesis, hence no adjustment was made for familywise Type I error rate (Sheskin 1996). Edge plots were grouped by the same sites used for CCA (20 sites, as the edge survey did not include the three sites dominated by trees). For each site, percent of each cover type was calculated. The same site soil and land-use data used for CCA were used here (however the AI variable was binary as the "logs in field" category was no longer applicable).

To further examine effects of soil and cover types on sapling invasion, I grouped soil types as low terrace (color gray or black and soil organic matter ≤ 6.8%) and high terrace (soil brown, organic matter ≥ 6.8%). Chi-square analysis was used to compare sapling counts of *Picea* (and separately of *Alnus*) among each of the 12 combinations of soil and cover types. Expected counts of the Chi-square analysis were calculated from the null hypothesis that there is no difference in sapling densities among soil and cover types. Hence, the mean total density in trees/ha was multiplied by the number of ha sampled in each category to determine expected number of trees for that category.

Results

Total counts within the edge plots produced 334 *Picea sitchensis* saplings (only 3% found on logs), 134 *Frangula purshiana*, 128 *Alnus rubra*, 13 *Tsuga heterophylla* (2 on logs), 5 *Salix scouleriana* and 5 *Pyrus fusca*. Frequency of occurrence in plots was 19.0% for *Picea*, 19.0% for *Frangula*, and 18.6% for *Alnus*. Most saplings occurred within 5 m of the forest edge (*Picea*, 56%; *Frangula*, 66%; *Alnus*, 68%). There were evident signs of browsing on 72% of *Alnus* saplings, 31% of *Tsuga*, and 18% *of Frangula* and none of *Picea*. Most *Tsuga* were of the smallest size class (0.50 - 0.75 m tall), while the median size class for *Picea* was 1.5 - 2 m tall. Most *Alnus* saplings were "bushy," indicating browsing.

Spearman rank correlations indicated that *Picea* sapling density was positively correlated with *Pteridium* cover type, *Anthoxanthum* cover, higher soil organic matter, higher soil moisture, higher soil acidity, and burning prior to clearing (Table 4.6). *Picea* sapling density was negatively correlated with intensity of agricultural disturbance, *Cirsium* cover, and *Agrostis* cover. *Alnus* sapling density showed no relationship with cover type or soil characteristics. Characteristics associated with *Frangula* invasion were similar to those of *Picea*.

Picea sapling invasion was almost confined to high-terrace soils (Table 4.7). Saplings were rare or absent on low terraces regardless of cover type. On high terraces, saplings were uncommon with *Agrostis*, *Carex*, *Cirsium*, or *Rubus* cover type, even though many plots abutted mature *Picea* forest. This result is concordant with lack of *Picea* in these cover types in 1997 field survey (Table 4.1, Fig. 4.2). On high terraces, only *Anthoxanthum* or *Pteridium* supported substantial *Picea* invasion. In contrast, *Alnus* invasion was greater on lower terraces.

Discussion

Factors that influence Picea *invasion*

The vegetation analyses suggest that colonization of the Queets fields by *Picea* may be affected by soils, plant cover, burning prior to clearing, and past agricultural use. *Picea* establishment was essentially restricted to high-terrace soils. Soil properties that changed with terrace age were percent moisture, organic matter, and pH. Fonda (1974) speculated that increased summer water retention was the most important soil change accompanying terrace development. In my experimental studies (Ch. 6), summer droughts limited *Picea* seedling establishment. The increase in soil organic matter on higher terraces increases available water capacity for plants (Hudson 1994). In addition to its effect of increasing water retention, soil organic matter may be directly conducive to *Picea*, which usually establishes on debris atop nurse logs in local forests (McKee et al. 1982). Fonda (1974) concluded that the decrease in pH with higher terraces was the result, and not the cause, of the change from deciduous to coniferous species.

Picea invasion of high-terrace sites was concentrated in sites dominated by *Anthoxanthum* or *Pteridium*. Why are grassy meadows of *Anthoxanthum* more invasible than those of *Agrostis*? Competition for space and soil resources may be greater between emergent *Picea* and the sod-forming *Agrostis* than with the bunchgrass *Anthoxanthum*. Other studies in old fields have shown that tree establishment can be inhibited by competition from herbs (De Steven 1991b, Myster 1993, Berkowitz et al. 1995). Smit & Olff (1998) found that woody species colonization of old fields occurred more rapidly on nutrient-poor soils, where perennial herbs were less abundant. In my fields, *Anthoxanthum* may indicate less fertile soil. The association of *Pteridium* with *Picea* may involve direct or indirect facilitation (*sensu* Levine 1999). *Pteridium* may directly provide shade to *Picea* seedlings during time of drought, or *Pteridium* may indirectly promote *Picea* invasion by reducing the abundance of *Agrostis*. Werner and Harbeck (1982) reported that *Rhus typhina* indirectly facilitated tree colonization of old fields by suppressing groundcover of herbaceous perennials. However, since *Picea* sapling invasion in my fields is higher in the grass *Anthoxanthum* than in *Pteridium*, an alternative hypothesis is that *Picea* and *Pteridium* simply have similar environmental preferences and that facilitation is not important. Why is *Picea* absent from patches of *Cirsium*, *Carex*, or *Rubus*? Stands of *Cirsium* do not suppress *Agrostis* cover. Dense patches of *Carex* or *Rubus* seem to exclude virtually all cover beneath them, which would include *Picea*. Tappeiner et al. (1991) reported that *Rubus spectabilis*, with clonal habits similar to *Rubus laciniatus*, can maintain a dense canopy that arrests succession in clearcuts or riparian areas unless disturbed.

Picea invasion of the Queets old fields is also related to prior land-use. Invasion is more likely in fields that were burned before clearing. This is in agreement with Peterson et al. (1997), who reported that slash burning benefits *Picea* regeneration. Burning also promotes *Pteridium* establishment (Page 1986), which may then facilitate *Picea*, as discussed above. Logs left in two Queets fields enhanced *Picea* invasion soon after abandonment. Harmon & Franklin (1989) found that nurse logs accounted for most of the regeneration of *Picea* within the Olympic rain forest because regeneration on the forest floor was inhibited by competition from herbs and mosses. *Picea* invasion was higher in Queets fields that were former pastures than those with evidence of past use for crops, indicating that degree of agricultural disturbance may have long-lasting effects. Similarly, in the eastern USA, species differences in tree colonization of old fields have been related to whether or not fields had been cultivated or pastured (Motzkin et al. 1996; Stover & Marks 1998).

Species assemblages and succession

The species composition of the Queets fields suggests that it has been influenced by elk herbivory (Table 4.1). Northern European pasture grasses and forbs covered the grassy meadows. The five major invading species (*Carex obnupta*, *Cirsium arvense*, *Pteridium aquilinum*, *Rubus laciniatus* and *Picea sitchensis*) are generally unpalatable to mammals (Grime et al. 1988) or avoided by elk (Happe 1993). Similar species composition has been reported from meadows grazed by elk within coastal redwood forests of Northwestern California (Harper 1962). Olff et al. (1999) described a mosaic of vegetation in lowland floodplains of Northwestern Europe that has been grazed by large mammals. This landscape is reminiscent of the Queets fields in that unpalatable species form patches among pasture herbs. In Europe, the unpalatable species facilitate invasion of palatable deciduous trees by protection or herbivore avoidance of their patches. However, in the Queets fields, *Cirsium, Carex* or *Rubus* show no sign of being invaded by other species. Within the centers of a few *Rubus laciniatus* patches are native rain forest shrubs (*Rubus spectabilis* and *Sambucus racemosa*) that are otherwise browsed by elk (Schreiner et al. 1996). However, there is no sign as yet of succession of these patches beyond a shrub stage. Where *Picea* trees did establish in the fields, they appear to have suppressed the ground cover of exotic pasture species and native understory species were present.

Agrostis gigantea has been the most successful survivor of the introduced pasture species. It is common in moist meadows in Britain (Grime et al. 1988) and in the Pacific Northwest. In contrast, *Anthoxanthum odoratum* and its associates, *Plantago lanceolata* and *Hypochaeris radicata,* occur on less fertile soils (Grime et al. 1988). The division of meadows in the Queets fields into *Agrostis* and *Anthoxanthum* associations suggests soil fertility differences, which were not measured in my soil analyses.

Assuming that pasture vegetation occupied the fields upon abandonment, parts of the Queets fields have changed in different pathways to *Carex*, *Cirsium*, *Pteridium*, *Rubus*, or *Picea*, while others have remained dominated by pasture herbs. Multiple pathways of succession have been demonstrated in several systems, which may reflect individualistic species behavior in a local context of available pool of species and environmental conditions (Glenn-Lewin & van der Maarel 1992; Fastie 1995).

Arrested succession

What factors have retarded the succession of fields to trees within the Olympic rain forest? Theories of plant succession emphasize population characteristics and interactions with the abiotic and biotic environment (Walker et al. 1986, Myster 1993). The life history characteristics of the dominant trees near these fields may not be well suited for colonization in these environments. *Picea*, *Alnus* and *Tsuga* have small seeds and appear ill adapted to establish in dense cover. *Alnus* germinates best on exposed mineral soil. Most *Picea* and *Tsuga* seedlings do not emerge until late spring in regional forests, grow slowly, are susceptible to summer drought and compete poorly with herbs (Gashwiler 1971, Harmon & Franklin 1989, Gray & Spies 1997). Prach et al. (1996) found that competition from dense herb cover prevented invasion of fields by *Picea abies* for over 50 years. In contrast, tree invaders of eastern USA fields are typically *Pinus* spp., with seeds 5 to 10 times larger than those found here, or large-seeded deciduous species. However, sixty-year-old fields with little woody invasion have been reported on Minnesota sand plains (Inouye et al. 1987), although dominants of local forests were large-seeded *Quercus* spp. Inouye et al. (1994) believed that drought stress, low soil nitrogen and, to a lesser extent, browsing by deer may retard succession in these fields. Elk browsing on the Queets fields may have depressed edge establishment by seedlings of *Tsuga* or *Alnus*, but the primary barrier to tree colonization operates before elk herbivory can be important, as newly-emergent tree seedlings were absent from most areas.

Summary

Picea invasion within these fields occurs primarily on older alluvial soils that have higher organic matter and moisture, where cover is dominated by the fern, *Pteridium*, or bunchgrass, *Anthoxanthum*. *Picea* invasion occurs predominantly on previously burned sites that had experienced less-intensive agriculture. Most sites lack these characteristics and hence exhibit arrested succession.

Plant cover or soil factors may directly affect tree colonization, while effects of past burning or agricultural use are indirect, through their historic influence on cover and soil factors. Both high-terrace soils and appropriate cover seem to be necessary for *Picea* invasion. Which factors are most important are difficult to infer from the correlative studies of this chapter. In the next two chapters, I explore the mechanistic basis of these relationships and evaluate their relative importance.

Table 4.1. Mean cover percentage of common species[1] in each cover type. Also listed are number of fields and number of quadrats in which cover types occurred. Nomenclature follows Kartesz (1994).

	Cover type[2]						
	AGGI	CIAR	ANOD	RULA	PTAQ	CAOB	PISI
number of fields (n = 11)	11	5	6	7	6	6	4
" of quadrats (n = 502)	227	45	59	39	67	26	39
Grasses - % cover							
Agrostis gigantea[3]	60	50	34	20	20	4	3
Anthoxanthum odoratum	6	<1	46	6	20	3	3
Dactylis glomerata	2	1	2	<1	1	<1	--
Elytrigia repens	2	<1	--	--	<1	--	--
Holcus lanatus	19	32	1	17	6	2	<1
Holcus mollis	4	--	<1	8	--	2	--
Poa pratensis[4]	4	1	1	1	1	<1	--
Sedges							
Carex obnupta[N]	<1	--	2	<1	10	97	<1
Forbs							
Cirsium arvense	7	51	<1	3	<1	7	--
Hypochaeris radicata	3	--	9	<1	6	<1	4
Plantago lanceolata	3	4	11	<1	3	<1	<1
Ranunculus repens	9	30	6	19	8	5	3
Stachys ciliata[N]	<1	<1	--	<1	1	<1	2
Trifolium repens	12	<1	2	4	<1	<1	--
Ferns							
Pteridium aquilinum[N]	4	--	17	17	73	8	19

Table 4.1 (continued)

	Cover type[2]						
	AGGI	CIAR	ANOD	RULA	PTAQ	CAOB	PISI
Shrubs							
Rubus laciniatus	2	--	<1	57	7	8	<1
Rubus ursinus[N]	<1	<1	<1	<1	8	6	11
Trees							
Frangula purshiana[N]	--	--	<1	--	2	--	1
Picea sitchensis[N]	<1	--	<1	--	<1	--	98

[1]Species included have > 2 % cover in at least one cover type; [2]Cover types defined by cluster analysis: AGGI = *Agrostis gigantea*, CIAR = *Cirsium arvense*, ANOD = *Anthoxanthum odoratum*, RULA = *Rubus laciniatus*, PTAQ = *Pteridium aquilinum*, CAOB = *Carex obnupta*, PISI = *Picea sitchensis*; [3]may include small amounts of *Agrostis capillaris*; [4]may include small amounts of *Poa trivialis*; [N]native species.

Table 4.2. Species ordination scores of first two axes of Detrended Correspondence Analysis of all quadrats, for species included in Table 4.1. Species are ordered by their scores on DCA-1.

	DCA-1	DCA-2
Cirsium arvense	-10	281
Elytrigia repens	8	184
Trifolium repens	49	165
Holcus mollis	83	305
Poa pratensis	107	179
Holcus lanatus	116	214
Agrostis gigantea	156	165
Dactylis glomerata	168	181
Ranunculus repens	223	262
Plantago lanceolata	231	71
Rubus laciniatus	284	330
Anthoxanthum odoratum	287	27
Hypochaeris radicata	331	-104
Carex obnupta	361	390
Pteridium aquilinum	384	39
Frangula purshiana	437	-392
Rubus ursinus	440	143
Stachys ciliata	442	274
Picea sitchensis	500	117

Table 4.3. CCA interset correlations (Pearson r) of environmental variables with canonical axes and Spearman rank correlations of environmental variables with DCA axes (n = 23 sites). As significance of interset correlations is problematic (McCune & Mefford 1997), DCA correlations are presented for additional evidence of relationships.; *P < 0.05; **P < 0.01

	CCA interset correlations		DCA rank correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
soil % water - *moisture*	0.64**	0.08	0.68**	- 0.29
soil % organic matter - *organic*	0.45*	- 0.41*	0.53*	- 0.53*
soil pH - *pH*	- 0.61**	0.46*	- 0.64**	0.59**
soil % sand - *sand*	- 0.22	- 0.46*	- 0.16	- 0.36
intensity of agricultural use - *AI*	- 0.84**	- 0.11	- 0.81**	0.11
burning before clearing - *burn*	0.62**	- 0.14	0.68**	- 0.27

Table 4.4. Characteristics of *Picea sitchensis* in the three sites with substantial invasion.

	Site 2M-PS	 2H-PS	 4H-PS
total hectares of site	3.1	0.8	0.8
% *Picea* cover	57	48	61
trees / ha (> 5 m tall)	75	33	50
% trees on nurse logs	48	50	0
saplings / ha (0.5 - 5 m tall)	79	21	150
% saplings on nurse logs	3	40	0

Table 4.5. Number of hectares sampled in 1998 Edge Survey as classified by cover and soil type. Plots were 10 x 20 m (0.02 ha). Low soil terraces include Fields 1L, 2L, 3L, 5L, 6L, 7L. High terraces include Fields 2M, 2H, 3H, 4H, 8H.

	soil terrace type	
	low	high
cover type	(n = 166 plots)	(n = 108 plots)
total cover	3.32	2.16
Agrostis gigantea	1.71	0.56
Anthoxanthum odoratum	0.06	0.29
Cirsium arvense	0.43	0.27
Carex obnupta	0.22	0.10
Pteridium aquilinum	0.26	0.80
Rubus laciniatus	0.57	0.10

Table 4.6. Spearman rank correlations of edge sapling density with characteristics of 20 sites. *P < 0.05; **P < 0.01

	Saplings per ha		
Site characteristic	*Picea sitchensis*	*Alnus rubra*	*Frangula purshiana*
percent cover type of edge plots			
Agrostis gigantea[1]	- 0.42*	0.30	- 0.55*
Anthoxanthum odoratum[1]	0.58**	- 0.37	0.38
Cirsium arvense[1]	- 0.55**	0.07	- 0.55*
Carex obnupta[1]	- 0.18	- 0.22	- 0.09
Pteridium aquilinum[1]	0.60**	- 0.24	0.69**
Rubus laciniatus[1]	- 0.23	- 0.03	0.16
site environmental variables			
soil % water[1]	0.54*	- 0.18	0.55*
soil % organic matter[1]	0.74**	- 0.26	0.51*
soil pH[1]	- 0.46*	0.08	- 0.38
soil % sand	- 0.02	0.00	- 0.21
AI index[1]	- 0.51*	0.45*	- 0.87**
BURN index[1]	0.48*	- 0.36	0.81
percent of forest canopy adjacent to edge plots			
Picea sitchensis	0.81**	- 0.34	- 0.52*
Alnus rubra	- 0.72**	0.37	0.63**

[1] 1-tailed H_0 for correlation with *Picea* generated *a priori* by ordination analysis; H_0 for remaining correlations are 2-tailed

Table 4.7. Mean sapling densities of *Picea sitchensis* and *Alnus rubra* in edge areas classified by cover and soil type (see Table 4.4 for number of ha sampled in each category). χ^2 test compared observed sapling counts with counts expected in the 12 categories under the H_0 that sapling densities are equal in all categories.
$\chi^2 = 1247$, $P < 0.001$ for *Picea*; and $\chi^2 = 82$, $P < 0.001$ for *Alnus*.

	Picea per ha		*Alnus* per ha	
	soil terrace type		soil terrace type	
cover type	low	high	low	high
Agrostis gigantea	1	16	47	0
Anthoxanthum odoratum	0	406	0	0
Cirsium arvense	0	4	2	4
Carex obnupta	0	10	32	0
Pteridium aquilinum	4	242	30	18
Rubus laciniatus	0	0	11	0

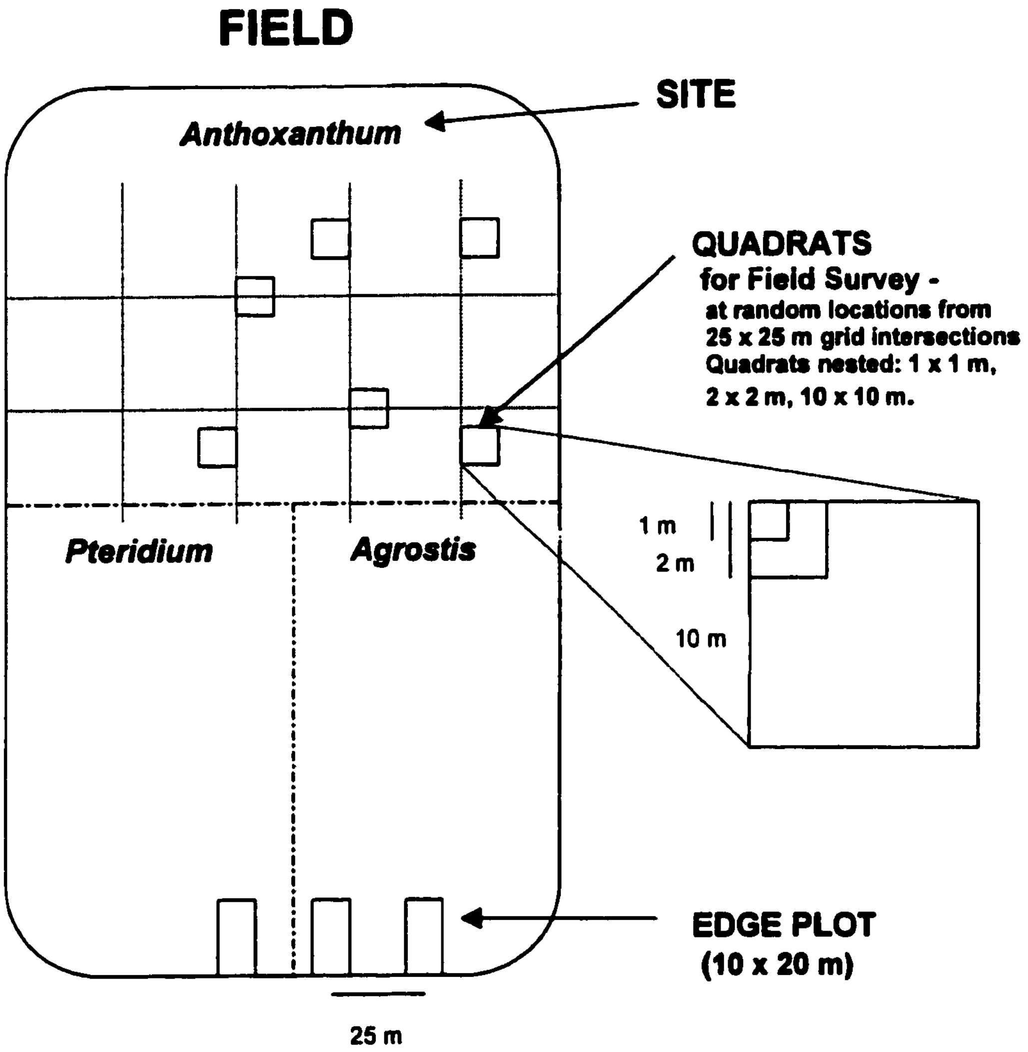

Figure 4.1. Sampling scheme and terminology for vegetation analysis. Fields were divided into 1- 3 sites for CCA, which are labeled by dominant cover type (*Agrostis*, etc.). Quadrats for vegetation sampling in the field survey were located at random distances (0 – 9 m) from intersections of 25 m square grid lines. (Quadrats to the north of the intersections were placed to the east, those south to the west, to prevent the possibility of overlap.) Smaller quadrats were nested within 10 x 10 m quadrats. Plots for the edge survey were located every 25 m along the forest edge. They were 10 m wide and extended 20 m into the field. (Although only a few are drawn here, quadrats and edge plots were located throughout field.)

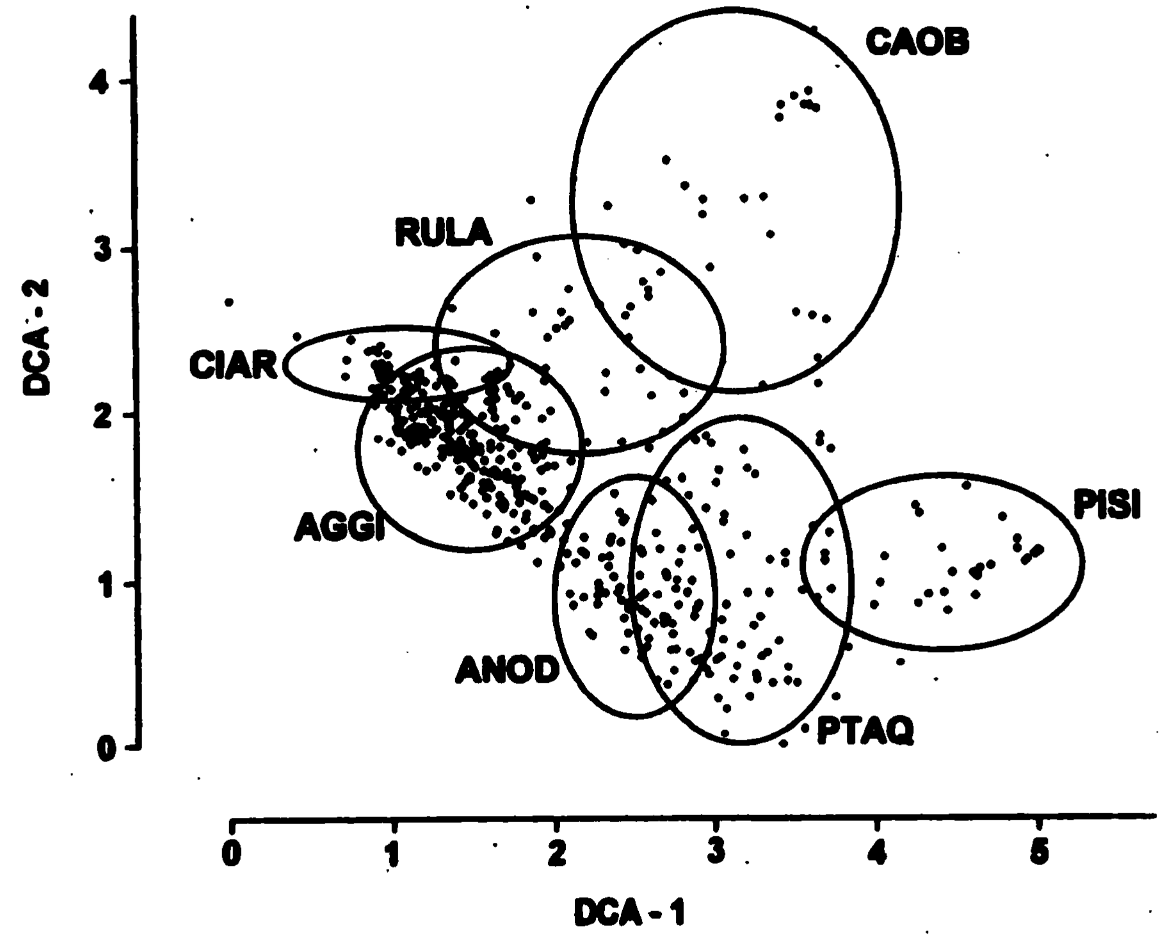

Figure 4.2. Detrended Correspondence Analysis of all quadrats: distribution of plots along axes 1 and 2. Each oval circumscribes distances ± 2 standard deviations on axes 1 and 2 from the centroid of quadrats of indicated cover type, calculated from the coordinates of all quadrats within the type. Code: AGGI - *Agrostis gigantea*, ANOD - *Anthoxanthum odoratum*, CAOB - *Carex obnupta*, CIAR - *Cirsium arvense*, PTAQ -*Pteridium aquilinum*, RULA - *Rubus laciniatus*, PISI - *Picea sitchensis*. Eigenvalue of DCA-1 = 0.72; DCA-2 = 0.46. Total variance (inertia) = 3.68.

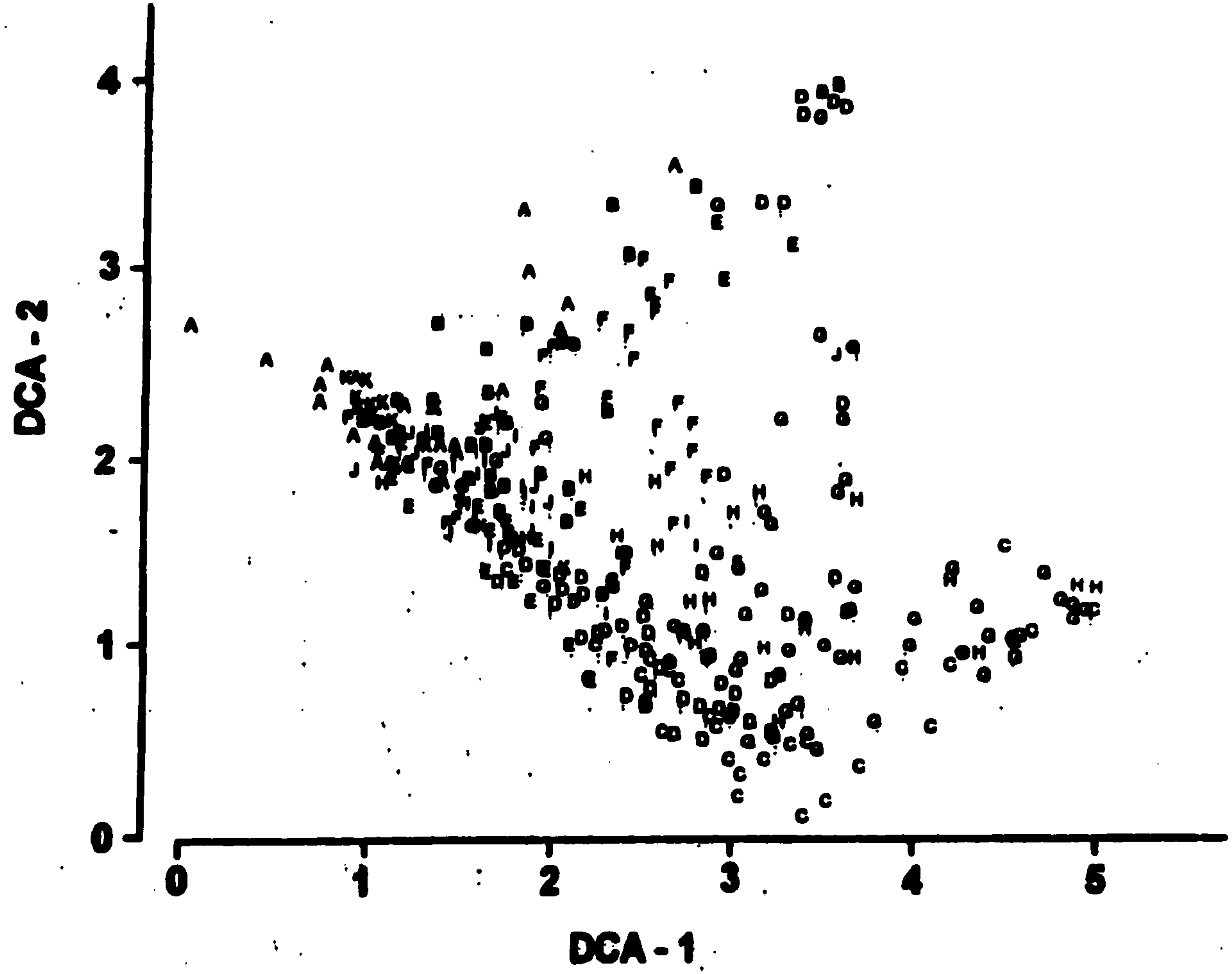

Figure 4.3. Detrended Correspondence Analysis of quadrats: grouped by field. (See Fig. 4.2 for DCA grouped by cover type). Field groups show high overlap. Large fields with many cover patches, such as D and G, have quadrats spreading through much of ordination. Field code: A = 6L, B = 7L, C = 4H, D = 3H, E = 3L, F = 2L, G = 2M, H = 3H, I = 1L, J = 5L, K = 8H. Some of the same printed letters that overlapped were removed from display for clarity.

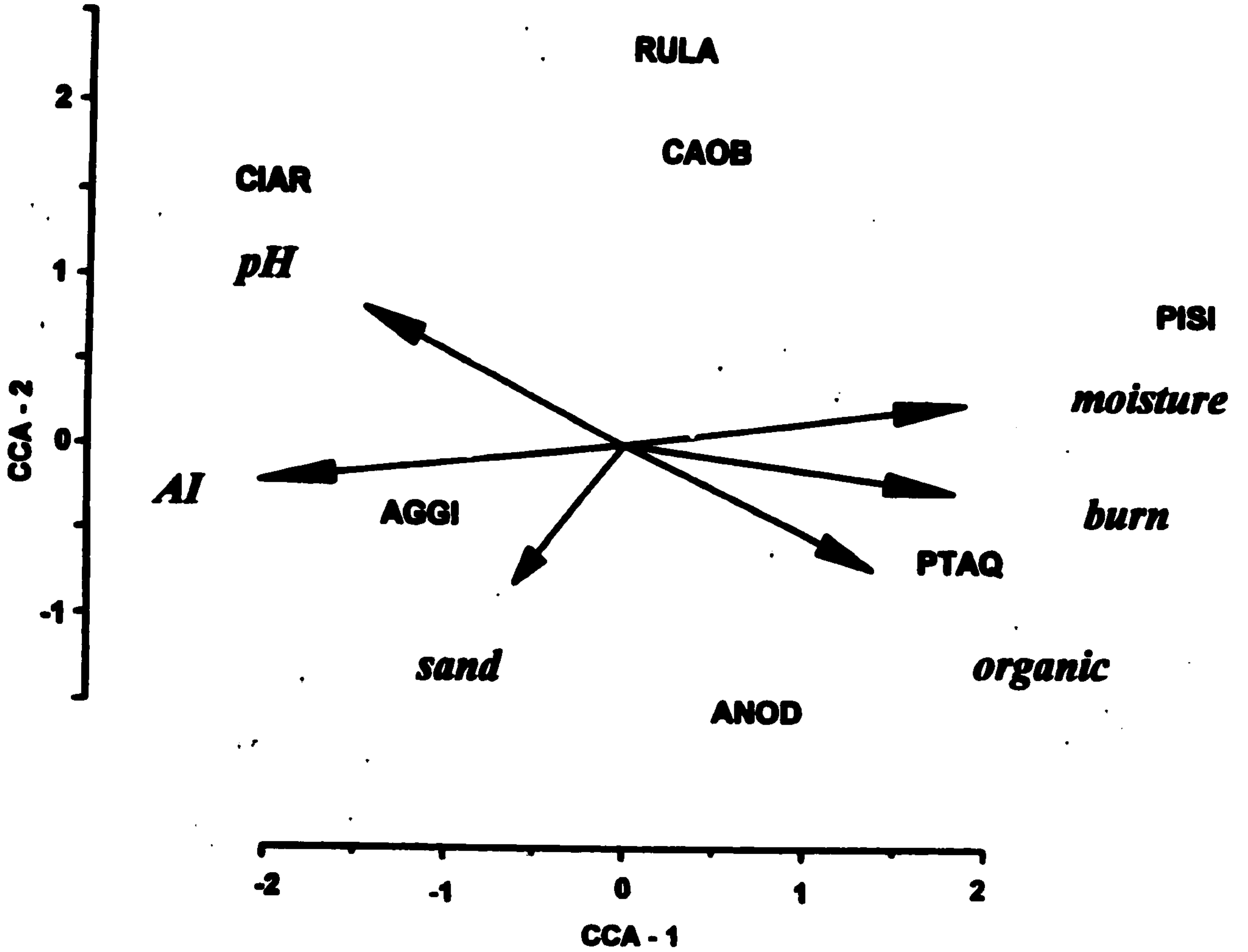

Figure 4.4. Canonical Correspondence Analysis: biplot of environmental variables and distribution of seven dominants on species ordination. (Locations of 23 sites not shown on ordination.) See Fig. 4.2 for species codes. See Table 4.2 for environmental variables code. Eigenvalue of CCA-1 = 0.41; CCA-2 = 0.13.

5. EFFECTS OF PLANT COVER AND SOIL ON INVASION OF OLD FIELDS BY *PICEA SITCHENSIS*

Introduction

Competition from herbaceous cover and soil resource limitations are two of many factors that may deter tree colonization of old fields (Tilman 1988, Gill & Marks 1991, Myster 1993, Li and Wilson 1998). Competitive intensity should logically vary among different types of cover. Burton and Bazazz (1991) found that seedling emergence among tree species varied with vegetation types in old fields. The intensity of competition between tree seedlings and associated vegetation varied widely among cover types in the study of Berkowitz et al. (1995). Studies of the influence of local soil differences on tree invasion are less common (Myster 1993). Smit & Olff (1998) found that regional soil differences affected the rate of woody plant invasion of fields. They concluded that fields with nutrient-rich soils supported dense herbaceous cover that inhibited invasion. However, Burton and Bazazz (1991) reported that differences in local soil type did not affect seedling emergence.

Differential tree invasion of old fields in the Queets River Valley, Olympic National Park allowed me to examine the association between vegetation or soil conditions and colonization. *Picea sitchensis* is the most successful tree invader. Vegetation analyses (Ch. 4) suggested that *Picea* invasion was more likely along edges with higher soil organic matter (SOM) and moisture and where plant cover was dominated by *Anthoxanthum odoratum* or *Pteridium aquilinum*. Invasion was rare along edges dominated by *Agrostis gigantea*. The goals of this study were to examine hypotheses involving this process at a finer scale and to evaluate which cover or soil factors were best related to *Picea* sapling invasion.

In Chapter 4, I suggested that *Agrostis* is less invasible than either *Anthoxanthum* or *Pteridium* because it provides more competition to *Picea* seedlings. In this study, I examine aspects of plant cover that may be indicators of degree of competition: total plant cover, ground cover (total plant cover minus layer of fern or shrub cover), and depth of thatch and sod. This leads to Hypothesis 1: *Agrostis* cover is positively associated, and *Anthoxanthum* negatively associated, with an increase in total plant cover, ground cover, thatch thickness, and sod thickness.

In Chapter 4, I also speculated that *Pteridium* foliage might decrease other cover beneath it. Hence, Hypothesis 2: *Pteridium* is negatively associated with *Agrostis* and ground cover.

Noting that drought was common during summers in the Queets fields at the time when *Picea* saplings emerge, I speculated that moisture retention might be the most important soil factor related to colonization. Thus, Hypothesis 3: soil available water capacity (AWC), as estimated from soil organic matter (SOM) and soil texture, is better correlated with *Picea* sapling invasion than other individual measures of soil characteristics (SOM alone, soil particle size, soil % water).

Considering the small size of *Picea* seeds, I propose Hypothesis 4: *Picea* is negatively correlated with litter or moss cover. The finding that intensity of past agricultural disturbance was negatively correlated with *Picea* in Chapter 4 led to Hypothesis 5: *Picea* invasion is associated with the presence of native herbs (indicators of areas with less past disturbance).

Methods

Nine study plots were chosen subjectively along field edges to represent different degrees of *Picea* sapling invasion and a variety of vegetation types and soils. All plots bordered stands of mature *Picea*, and should have received an ample seed rain over the years. To see if sapling invasion varied with amount of *Picea* in the adjacent forest canopy, the area of *Picea* canopy > 5 m in height that faced each plot was measured trigonometrically (cone production is limited in trees < 5 m; Peterson et al. 1997).

Plots were chosen *a priori* for specific contrasts. Plots 1L and 3L (plot names taken from field name, see Ch. 2 & App. 3 for field information) were low-terrace reference plots lacking significant *Picea* invasion. The 1998 edge survey (Ch. 4) showed that *Picea* invasion is rare on low alluvial terraces. The remaining seven plots were chosen to represent varying degrees of invasion on higher terraces. Plots 1M and 3H were chosen because they were on higher terraces adjacent to old-growth *Picea*, yet showed little invasion. Plot 4H was chosen for its high degree of invasion. Two pairs of plots (2Ma vs. 2Mb and 3Ha vs. 3Hb) were chosen because plots within each pair showed differential invasion but were located within the same sites, as defined in Ch. 3 (Sites 2M-PA & 3H-AO). Plots were examined 9 September - 1 October 1999.

The forest edge was defined as the edge of continuous tree canopy. The 1998 edge survey indicated that most *Picea* saplings were established within 5 m of this edge. Therefore, plots were 50 m long (parallel to the edge) and 5 m wide (Fig. 5.1). All saplings ≥ 25 cm tall were counted and their heights measured. Saplings ranged from 25 - 350 cm tall (~ 4-14 yr old, estimated from growth rates in my permanent quadrat studies).

Ten 1-m^2 quadrats were randomly located within the plots for measurements of plant cover. Locations directly under the crown of larger *Picea* saplings were excluded, since the goal was to measure effects of the environment on *Picea*, not *vice versa*. However, this raises the question of whether there were significant differences in environmental conditions between microsites where *Picea* saplings became established during the past ~4-14 yr and the sampled quadrat locations. Plant cover data from Williams (1975) and del Moral (1985) show that species composition of the fields, including areas of grass dominance by *Agrostis* or *Anthoxanthum*, has changed little in 25 years. Furthermore, although I chose to measure only saplings ≥ 25 cm tall for an indication of successful establishment, areas that contained large saplings also contained recently-emergent seedlings, which were included in quadrat placement.

At each quadrat, percent cover of each plant species other than *Picea* was estimated. Plant nomenclature follows Kartesz (1994). Total plant cover is defined as the sum of all individual species cover (and thus may exceed 100%). Ground cover is defined as total cover minus cover of those species (*Pteridium aquilinum*, *Rubus laciniatus*, and *Vaccinium parvifolium*) that formed a canopy above the ground surface. Depths of thatch, litter, and sod were measured. Thatch is a layer of interlocking grass stems and leaves above the soil surface. Litter is composed of detached plant remains. Sod is a layer of surface soil held together by matted roots.

Soil samples were collected at 5 to 15 cm below the surface in the 10 quadrats per plot during a dry period. In the laboratory, portions (~40 g) of each sample were oven dried at 105° C for gravimetric water content and combusted at 450° C for SOM content. Other portions (~50 g) were air dried, rolled, and passed through a 2-mm sieve to determine gravel content. Subsequent soil fractions (sand, silt, clay) were determined by the hydrometer method (Bouyoucos 1951). Available water content (AWC) was estimated for each sample to assess the relative ability of plots to resist drought. AWC was estimated from the equation of $\% \text{ AWC} = .3858 - 0.003 * \% \text{ sand} - 0.0027 * \% \text{ clay} + 0.0159 * \% \text{ SOM}$, of Rawls et al. (1992) for the difference in water retention between - 10 and - 1500 kPa. As this equation did not consider gravelly soils and their reduced water retention, I included gravel content in the "% sand" value for the AWC estimate.

For analysis of vegetation among plots, plant cover data from the nine plots (the mean of ten random quadrats per plot) were classified by Ward's agglomerative method, using a similarity coefficient of squared Euclidean distance (McCune & Mefford 1997).

Hypotheses were initially examined by Spearman rank correlation to investigate the association of *Agrostis*, *Anthoxanthum*, or *Pteridium* with certain cover characteristics (Hypotheses 1 & 2) and to assess relationships between numbers of *Picea* saplings and mean environmental measurements of the nine plots (Hypotheses 3, 4, & 5).

To examine which cover and soil factors showed the strongest correlations with *Picea* invasion, selected contrasts were conducted between plots or groups of plots that differed in degree of invasion (for the cover or soil variables, n = 10 per plot). Multiple contrasts were conducted by the Scheffe test after one-way ANOVA (Zar 1996). Single plot-to-plot contrasts were assessed by *t*-tests. Soil gravel content was not normally distributed and analyzed by nonparametric Mann-Whitney tests. Loglinear regression models were constructed of *Picea* saplings with the variables found to be most important in the previous analyses. Distribution of *Picea* sapling numbers among the plots was lognormal.

Results

The vegetation of the quadrat samples included 33 vascular species, four bryophytes, and one lichen (see App. 2 for complete list). Cluster analysis of the nine plots (Fig. 5.2) yielded two groups that corresponded to different levels of *Picea* invasion (Table 5.1). Fusion into two groups was very clean at 50% information remaining (Fig. 5.2). Grass cover was dominated by *Anthoxanthum* in the invaded group (A) and *Agrostis* in the group with little invasion (B). Of the subdominants, *Hypochaeris radicata* was associated with Group A. *Ranunculus repens* and *Holcus lanatus* were associated with Group B. *Pteridium* was more abundant in Group A but also was a co-dominant with *Agrostis* of one plot (1L) in Group B. The *Agrostis-Ranunculus-Holcus* content in Plot 1L explains its fusion with Group B, even though *Pteridium* is abundant. The two higher-terrace plots with little *Picea* invasion (Plots 1M, 2H) were similar in composition. Both had > 30% cover of *Anthoxanthum*, but also had high cover of *Agrostis* and *Ranunculus* and thus fused with the low terrace plots (Fig. 5.2.)

Number of *Picea* saplings per 250-m^2 plot ranged from 0 to 106 (Table 5.1). Most saplings were 25-50 cm tall. Degree of *Picea* sapling invasion in the plots was not correlated with the area of adjacent *Picea* forest canopy facing the plots (Spearman $r_s = -0.25$, $P > 0.50$, $n = 9$).

In accord with Hypotheses 1 and 2, Spearman rank correlations indicated that *Agrostis* cover was correlated with thickness of sod and thatch ($P < 0.01$) and amount of ground cover ($P < 0.05$), while *Anthoxanthum* was negatively correlated with these characteristics (Table 5.2). However, total ground cover was not correlated with *Agrostis*. Contrary to Hypothesis 2, *Pteridium* was not associated with a decrease in *Agrostis* or in ground cover. *Pteridium* was correlated with total cover, as might be expected because it forms the primary field canopy layer.

As in my previous study (Ch. 4), the degree of *Picea* sapling invasion was negatively correlated with *Agrostis* cover and positively correlated with *Anthoxanthum* (Table 5.3: both with $P < 0.01$). However, in contrast to the previous study, *Picea* was not significantly correlated with *Pteridium* among the nine plots in this study.

Hypotheses 4 and 5 were not supported. *Picea* was not significantly correlated with moss or native herb cover. Mean litter thickness was not related to *Picea*. Litter cover in the plots was often thin and discontinuous.

Among the soil properties measured, *Picea* showed the strongest correlation with organic matter (Table 5.3). Contrary to Hypothesis 3, available water capacity (AWC), estimated from an equation that incorporates organic matter and particle size, did not improve the correlation. Soil particle size showed no relationship to *Picea*. The correlation obtained between *Picea* and estimated AWC is largely due to the SOM component of the equation. In contrast to the results of Chapter 4, *Picea* did not vary with soil water percentage.

Major factors found important to *Picea* invasion (*Agrostis* cover, *Anthoxanthum* cover, SOM, characteristics related to soil moisture) were examined by specific multiple and single plot contrasts (Table 5.4). The five most invaded plots (Table 5.1: Group A) significantly differed from the other four plots by *Agrostis* and *Anthoxanthum* cover and SOM (Contrast 1). The two plots with the highest invasion differed from the next three (Contrast 2) by having less *Agrostis* and more SOM. In all three single plot-to-plot contrasts, mean *Agrostis* cover was lower in the more invaded plot, although significantly lower only in Contrast 5. SOM did not show a positive correlation with *Picea* invasion in these three contrasts and was negatively correlated with *Picea* in Contrast 3. Soil moisture properties usually were not important, although *Picea* invasion was lower on drier, gravelly soils in Contrast 4. In Contrast 5, *Picea* invasion was lower in the plot with higher moisture (Plot 2Mb, with the highest estimated AWC of all 9 plots).

The analysis of plot contrasts pointed to *Agrostis* cover and SOM as the most important factors related to *Picea* invasion. The combined effects of these two factors are illustrated in Fig. 5.3. SOM and *Agrostis* cover provided similar significant fits in simple linear regressions with log number of *Picea* saplings (Table 5.5). A multiple regression model that included both SOM and *Agrostis* explained the most variation. However, these two variables were not independent and inversely correlated ($r_s = -0.67$, $P < 0.05$, $n = 9$).

Discussion

Picea invasion was negatively associated (by rank correlation, plot contrasts, and regression) with abundance of the sod-forming grass *Agrostis*. Characteristics that may indicate degree of competition (ground cover, thatch, sod) were positively correlated with *Agrostis*. Areas of *Picea* invasion were correlated with cover dominated by the bunchgrass *Anthoxanthum*, which does not form either sod or thatch.

Competition from *Agrostis* and its associates, such as *Ranunculus* and *Holcus*, appears to be a major inhibitor of colonization of the Queets old fields by *Picea*. *Picea* seedlings do not emerge until May or June (Ch. 6), by which time grasses are lush and tall. Absorption by the dense mat of fibrous roots may limit the water and nutrients necessary for germination of the small *Picea* seeds or subsequent growth of seedlings. Late summer droughts, typical of the region (Fonda 1974) will exacerbate the competition for water. The increased ground cover and thatch in *Agrostis* communities will also depress the light available for growth of *Picea* seedlings.

The suppression of *Picea* invasion by *Agrostis* cover underscores the importance of herbaceous competition as an inhibitor of tree colonization of old fields (DeSteven 1991b, Gill & Marks 1991, Hill et al. 1995) and provides insight into the nature of competition in this system. Turf-forming grasses with a sod of matted roots, dense ground cover, and thatch present a formidable barrier to seedling establishment, especially to small-seeded species. Prach et al. (1996) reported that turf removal was necessary for natural seedling establishment of *Picea abies* in experiments in a 50-year-old sodgrass field in the Czech Republic. Coates et al. (1993) found that sodgrass reduced growth rates of *Picea sitchensis* seedlings more than bunchgrass. Magee and Antos (1992) reported that reduction of herbaceous vegetation is needed for *Abies procera* to invade edges of mountain-top meadows in the Oregon Coast Range. Tilman (1993) noted that herbs in more productive habitats can also inhibit colonization by decreased light penetration.

In this 1999 edge study, *Pteridium aquilinum* cover did not seem to influence *Picea* invasion; whether the vegetation beneath *Pteridium* was dominated by *Agrostis* or *Anthoxanthum* was more important. The suggestion of Ch. 4 that *Pteridium* may be associated with a reduction of *Agrostis* was not supported by this study, as *Agrostis* cover did not inversely correlate with *Pteridium*. The correlation between the *Pteridium* cover type and *Picea* saplings in the 1998 edge survey (Table 4.4) may have reflected the domination of the ground layer by *Anthoxanthum* within the invaded *Pteridium* cover type on the high terraces.

What influences whether or not grasslands in the Queets fields were dominated by *Agrostis* or *Anthoxanthum*? In other studies, *Agrostis gigantea*, *Ranunculus repens* and *Holcus lanatus* (Table 5.1: Group B) have been associated with fertile soil, while *Anthoxanthum odoratum*, *Hypochaeris radicata*, and *Plantago lanceolata* (Table 5.1: Group A) have been associated with areas of reduced fertility (Beddows 1961, Cavers et al. 1980, Turkington & Aarson 1983, Grime et al. 1988, Klinka et al. 1989, Lovett-Dust et al. 1990). In a 14-yr study of Netherlands hay fields in which soil nutrients declined after cessation of fertilizer input, Olff and Bakker (1991) found a reduction in cover of the initial dominants *Holcus lanatus* and *Agrostis stolonifera* (a close relative of *A. gigantea*) and an increase in *Anthoxanthum odoratum* and *Plantago lanceolata*. Other studies have linked *Anthoxanthum odoratum* with potassium-deficient soils (Thurston 1969, Wild et al. 1974, Luscombe et al. 1981).

I found no relationship between moss, litter, or native herb cover and *Picea* establishment. Moss cover was relatively sparse compared to the study of Harmon and Franklin (1989), which showed moss suppression of *Picea* sapling emergence in Pacific Northwest forests. Likewise, litter amounts were low compared to other studies. Litter is known to have multiple and contrasting effects on tree seedling establishment (Facelli 1994, Myster 1994), including inhibition of colonization by facilitating seed predation, inhibition by decreasing emergence, and facilitation by suppressing competing herbs. The range of native herb cover (0-5%) was too low to serve as a relative indicator of level of past disturbance or to influence *Picea* in other ways.

The increase of *Picea* invasion with SOM may be due to organic content directly, moisture retention, or coincidence. One or more other unidentified factors, which, like SOM, vary with age of alluvial terrace may be critical to *Picea* success. Since most *Picea* regeneration in Pacific Northwest forests occurs on decaying nurse logs (McKee et al. 1982), organic material may benefit germination and early growth. However, *Picea* also establishes well on mineral soils (Schopmeyer 1974, Peterson et al. 1997). The contribution of SOM to moisture retention (Hudson 1994) may be beneficial to *Picea* survival during summer droughts.

Burton & Bazazz (1991) found plant cover a better predictor of tree seedling emergence than soil type in their study in eight communities and three soils in Illinois old fields. In the Netherlands, Smit & Olff (1998) concluded that tree invasion of old fields was inhibited by dense cover of perennial herbs, which in turn occupied rich sandy loam soil. Poorer soils had less herbaceous perennial cover and more tree invasion. Thus, it may be that plant cover directly affects tree establishment through competition, but soils indirectly affect establishment through their influence on the plant cover.

Results of this and my previous study (Ch. 4) suggested that the negative effect of *Agrostis* cover on *Picea* colonization may be greater than the positive effect of SOM. Moreover, areas from the 1998 edge survey that had both high *Agrostis* and high SOM showed little *Picea* invasion (Table 4.5). I have suggested that inhibition of *Picea* by the *Agrostis* cover type involves production of sod and dense surface cover. The next chapter reports on cover removal experiments that directly examine effects of competition by *Agrostis* on *Picea* seedling establishment.

Table 5.1. Number of *Picea* seedlings and mean percent cover of major species[1] in 250 m^2 edge plots. Cover groups classified by Ward's agglomerative method (Fig. 5.2). Plots ordered by *Picea* seedling density.

	Plots of Cover Group A					Cover Group B			
	3Ha	4H	2Ma	2Mb	3Hb	2H	3L	1L	1M
number of *Picea* seedlings	102	68	35	14	12	3	1	0	0
grasses & sedges (% cover)									
Agrostis gigantea	12	25	27	56	16	52	57	70	58
Anthoxanthum odoratum	53	43	41	39	52	34	8	0	31
Holcus lanatus	0	<1	1	2	0	11	36	21	2
Carex obnupta	5	10	8	0	0	<1	0	0	0
forbs									
Achillea millefolium	1	2	0	0	6	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	8	0	0
Hypochaeris radicata	27	34	8	<1	7	2	<1	2	9
Plantago lanceolata	2	7	3	<1	5	0	<1	<1	<1
Ranunculus repens	3	1	5	7	2	29	11	44	39
Trifolium repens	<1	5	0	0	0	0	8	<1	2
ferns									
Pteridium aquilinum	43	52	90	66	17	24	<1	71	27
mosses									
Polytrichum juniperinum	9	4	<1	35	13	10	0	0	0
Rhytidiadelphus loreus	15	5	11	20	25	13	16	23	35
shrubs									
Rubus laciniatus	0	2	2	13	2	5	0	14	2
Rubus ursinus	4	2	12	0	18	3	5	0	0

[1] species > 5% cover in at least 1 of the 9 plots

Table 5.2. Spearman rank correlations of environmental characteristics and percent cover of *Agrostis*, *Anthoxanthum*, and *Pteridium*. (n = 9 plots). *P < 0.05; **P < 0.01; ***P <0.001

	% cover *Agrostis*	*Anthoxanthum*	*Pteridium*
% *Agrostis* cover	---	- 0.97***	0.10
% *Anthoxanthum*	- 0.97***	---	0.02
% *Pteridium*	0.10	0.02	---
cm sod	0.79**	- 0.68*	0.21
cm thatch	0.86**	- 0.92***	0.01
ground cover	0.77*	- 0.67*	- 0.15
total cover	0.48	- 0.33	0.87**

Table 5.3. Spearman rank correlations of environmental characteristics and *Picea* sapling density. (n = 9) * P < 0.05; **P < 0.01

	r_s	range[1]
hypothesized negative effect		
% *Agrostis* cover	- 0.86**	12 - 70
cm thatch	- 0.78*	0.0 - 2.4
% ground cover	- 0.75*	120 - 180
cm sod	- 0.58	0.1 - 2.1
% moss cover	- 0.24	9 - 55
% total cover	- 0.15	157 - 250
% gravel[2]	- 0.07	0 - 22
% clay[2]	0.10	4 - 8
% sand[2]	0.17	36 - 68
cm litter	0.32	0.7 - 3.4
hypothesized positive effect		
% *Anthoxanthum* cover	0.87**	0 - 54
% soil organic matter (SOM)	0.86**	7 - 13
% soil available water content estimate	0.63*	30 - 43
% native herbs	0.36	0 - 5
% *Pteridium* cover	0.27	1 - 90
% soil water	0.25	26 - 51

[1] range of mean values for the 9 plots; [2] hypothesized negative effect because factor decreases soil available water content

Table 5.4. Contrasts between edge plots in environmental characteristics related to *Picea* invasion. Multiple contrasts (# 1 - 2) by Scheffe test after one-way ANOVA of plots. Plot to plot contrasts by *t* - test, except % gravel by Mann-Whitney test, *P < 0.05 , **P < 0.01, n = 10 per plot; ^{N}negative effect on *Picea* expected; ^{P}positive effect on *Picea* expected. Asterisks are placed on bottom number if opposite to expected effect. Group means of contrasts are tabulated.

Contrast number & plot numbers[1]		Contrast description	*Picea* saplings	% *Agrostis*^{N}	% *Anthoxanthum*^{P}	% soil organic matter^{P}	% soil water^{P}	% sand^{N}	% gravel^{N}
1	1 - 5	Cover Group A	47	27**	46**	11.1**	35	54	--
	6 - 9	Cover Group B	1	59	18	8.1	36	54	--
2	1 - 2	two highest *Picea*	85	18**	48	11.9**	35	58	--
	3 - 5	intermediate *Picea*	20	33	44	10.6	36	52	--
3	1	highest *Picea*	106	12	53	10.7	35	64	0.2
	2	second highest	68	25	43	13.0**	36	51	0.3
4	1	higher *Picea*, same site	106	12	53	10.7	35**	64	0.2**
	5	lower *Picea*, same site	12	16	52	10.3	26	69	22.0
5	3	higher *Picea*, same site	35	27**	41	10.6	38	53	0.2
	4	lower *Picea*, same site	14	56	39	11.0	43*	36**	0.2

[1] Plot key: 1 = 3Ha, 2 = 4H, 3 = 2Ma, 4 = 2Mb, 5 = 3Hb, 6 = 2H, 7 = 3L, 8 = 1M, 9 = 1L;

Table 5.5. Regression models of *Picea sitchensis* sapling abundance with soil organic matter and *Agrostis* cover.

log (#*Picea* per plot + 1) =	P	adjusted R^2
- 2.7 + 0.37* % soil organic matter (SOM)	0.0023	0.72
2.3 - 0.03* % *Agrostis*	0.0033	0.69
- 0.7 + 0.24*SOM - 0.01* % *Agrostis*	0.0018	0.84

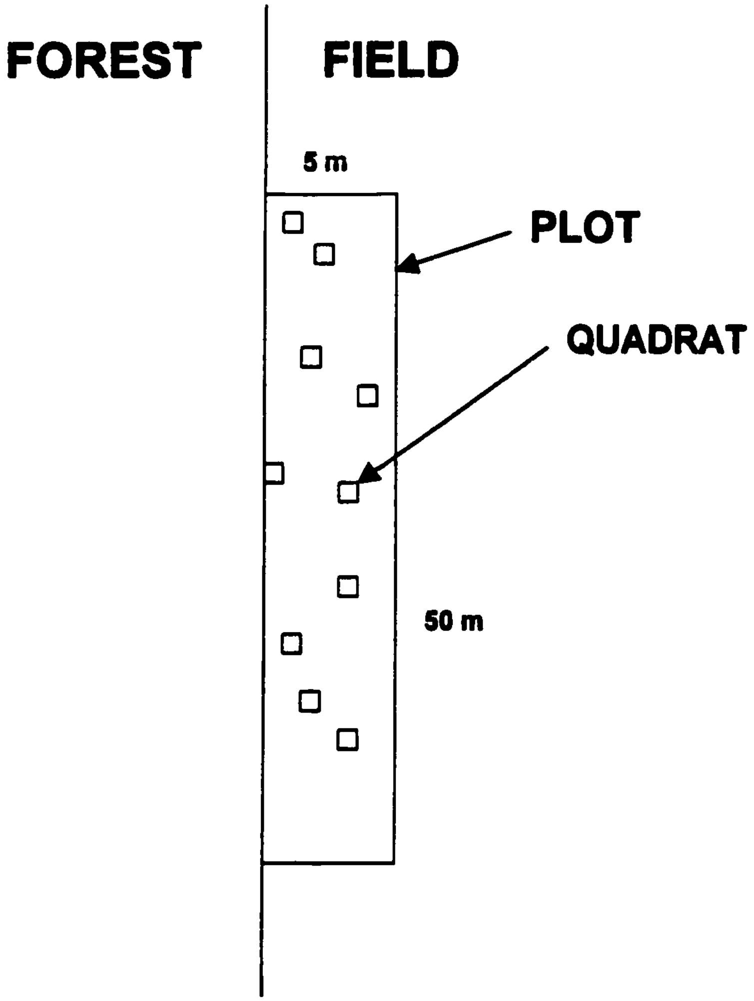

Figure 5.1. Sampling diagram and terminology for 1999 edge study. Plots were 50 m long, parallel with the forest edge and extended 5 m out into the field. Ten quadrats for cover and soil samples were randomly located within each plot.

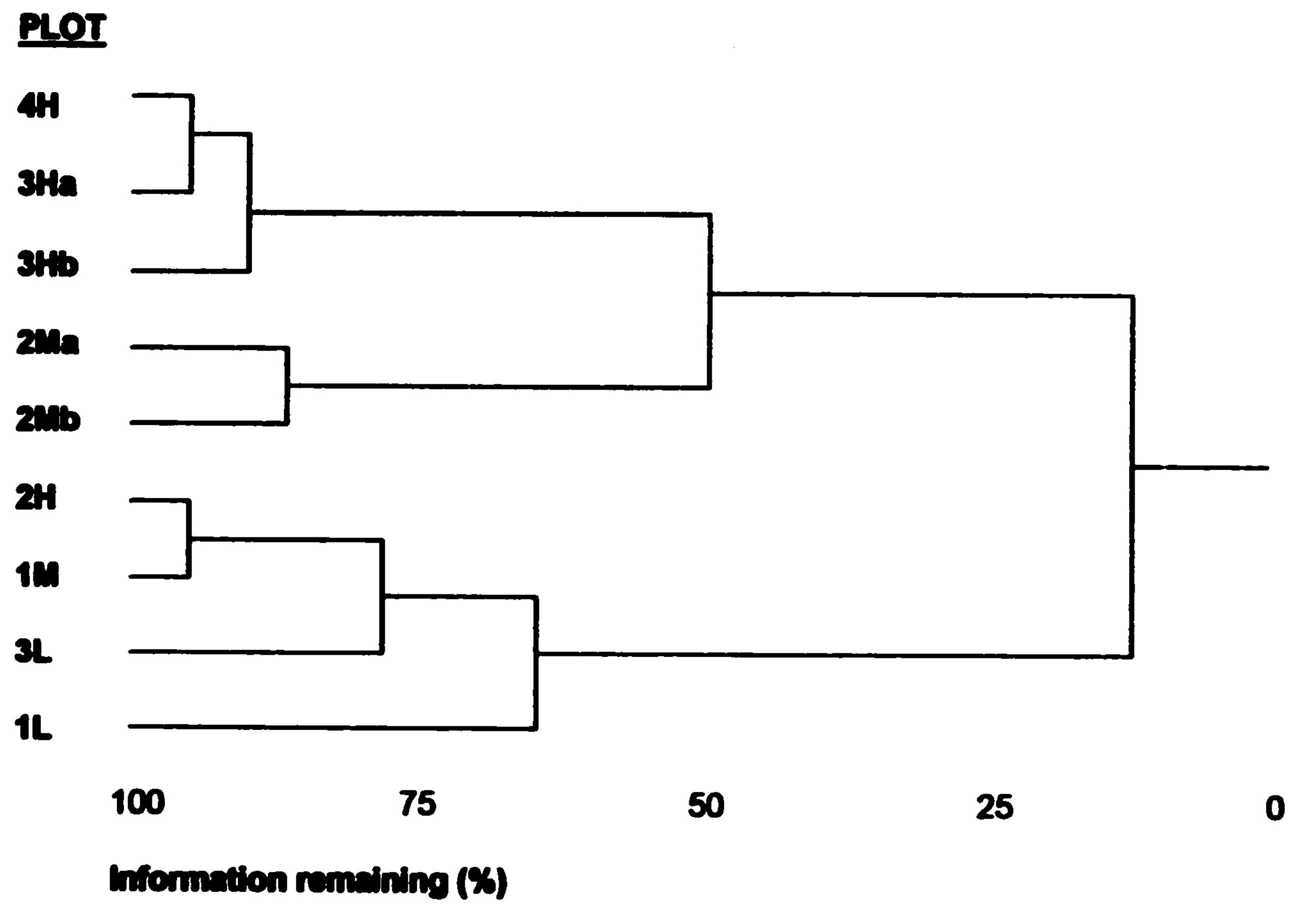

Figure 5.2. Dendrogram of cluster analysis of vegetation of nine edge plots by Ward's agglomerative method (McCune & Mefford 1997). Upper five plots in dendrogram designated as Group A in Table 5.1 (invaded by *Picea*); lower four as Group B.

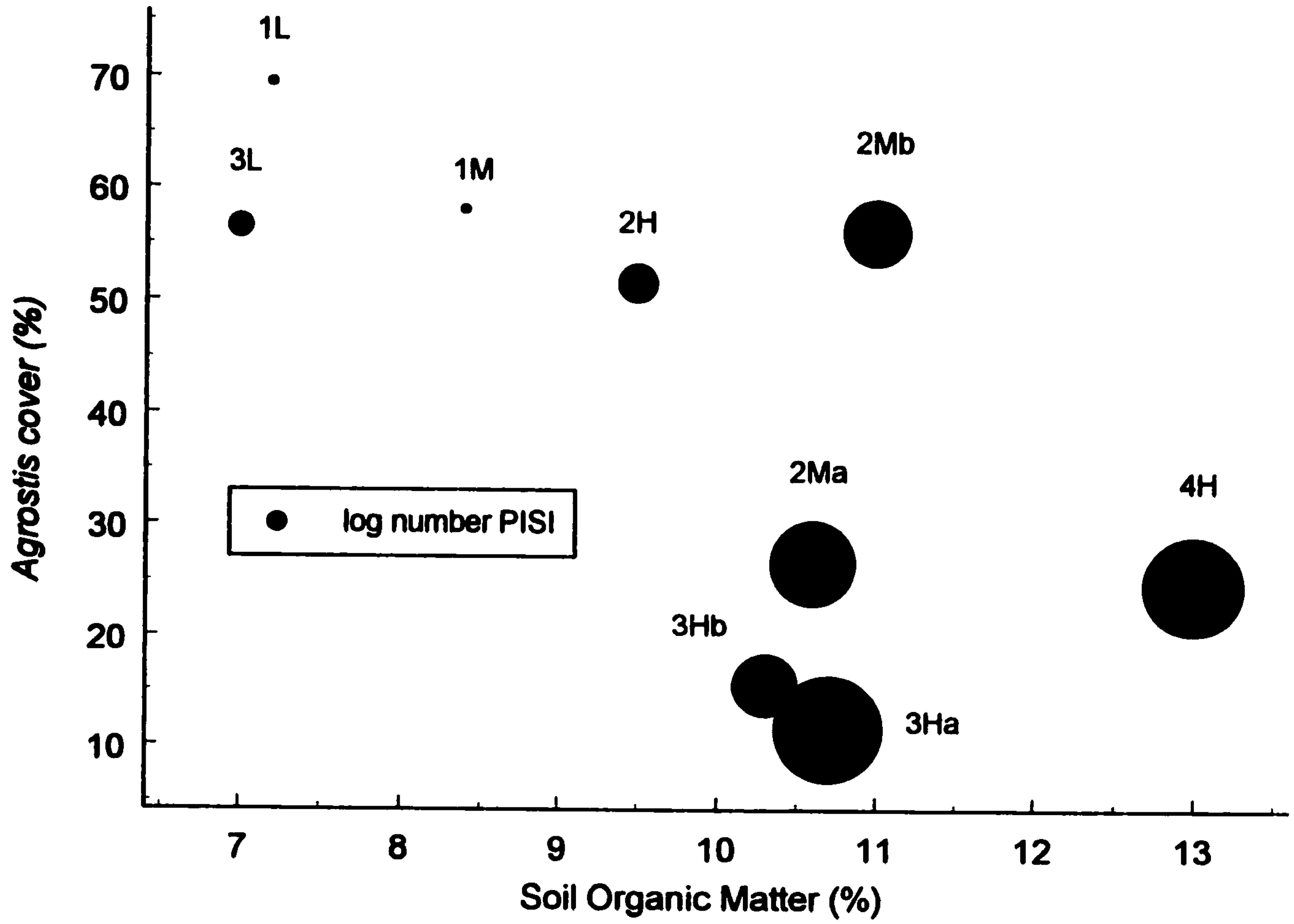

Figure 5.3. Effects of soil organic matter and % *Agrostis* cover on *Picea sitchensis* seedling invasion. Diameter of circles is proportional to log (number *Picea* seedlings + 1) for each 250 m^2 plot. (for circle size references: Plot 1L = 0 seedlings, Plot 3L = 1 seedling; Plot 3Hb = 12 seedlings, Plot 3Ha = 106 seedlings).

6. MECHANISMS THAT AFFECT TREE SEEDLING COLONIZATION OF OLD FIELDS

Introduction

For trees to establish in an old field, seeds must first reach the field, avoid predation, and germinate. Seedlings must survive in the face of competition and herbivory. Experimental studies have shown that tree establishment in old fields can be limited by rodent predation on seeds (Gill & Marks 1991, De Steven 1991a, Myster & Pickett 1993) or seedlings (Gill & Marks 1991, Ostfield & Canham 1993). Tree seedlings can be inhibited by competition from herbs (De Steven 1991b, Gill & Marks 1991, Berkowitz et al. 1995, Prach et al. 1996, Li & Wilson 1998). Seedling establishment may also be facilitated by herbaceous cover, particularly during drought stress (De Steven 1991b, Gill & Marks 1991, Berkowitz et al. 1995). Survival and growth of tree seedlings can be deterred by cervid herbivory (De Steven 1991b, Hill et al. 1995).

Old field succession in temperate forest biomes typically involves invasion by trees within a few decades. In the Queets Valley, Olympic National Park, tree colonization of sixty-year old fields is limited to a few areas. I designed experiments to test mechanisms that may inhibit or promote tree colonization in these fields and show how these mechanisms may be influenced by variation in plant cover.

Bordering the Queets fields are forests of *Picea sitchensis*, *Tsuga heterophylla*, or *Alnus rubra*, common dominant species of communities in Pacific Northwest temperate rain forests (Franklin & Dyrness 1973). The small, wind-blown seeds of these species disperse readily over distances equal to the size of the fields (Harris 1967), hence seed dispersal is not a limiting factor. This chapter describes experiments that investigate factors affecting the emergence, survival, and growth of introduced seeds and seedlings of *Picea*, *Tsuga*, and *Alnus* in the Queets fields. These factors include competition, rodent seed predation, cervid herbivory, and facilitation by *Pteridium*. In this chapter, each experiment is presented individually with an introduction, hypotheses, methods, and results. The reports of the five experiments are followed by a single discussion of all results.

General Methods

For seedling-emergence experiments, *Picea*, *Tsuga*, and *Alnus* seeds from the appropriate seed zone (012 - west side of Olympic Mountains) were obtained from Olympic National Forest, Olympia, Washington. Seeds were not stratified prior to sowing, because greenhouse trials indicated that stratification did not improve emergence.

Rates of seedling emergence in field soils in the greenhouse were 64% for *Picea*, 58% for *Tsuga*, and 44% for *Alnus*. In the 1999 seeding experiments (Table 6.1: 2-3), *Picea*, *Tsuga*, and *Alnus* seeds were mixed together and sown onto plots on two separate occasions at a density of 1600 / m^2 per species. Only a few *Alnus* seedlings were noted in any plot in my experiments, although they germinated successfully in the greenhouse. Therefore, results of seedling emergence experiments are confined to *Picea* and *Tsuga*.

Table 6.1 is a guide to my experiments and their locations. The layout of most experiments is illustrated in Fig. 6.1. Blocks of treatments were randomly located within sites. Sites are sections of fields dominated by a major cover type, as described in Chapter 4. Experiments were located within the three most common cover types (*Agrostis*, *Pteridium*, and *Anthoxanthum*) in Fields 1L, 2M, and 3H. Field 1L represented low-terrace gray soils, and Field 3H high-terrace brown soils with higher organic matter (Ch. 4). Soils in Field 2M were intermediate in color with heavier texture. Each field contained areas of *Pteridium* and *Agrostis* cover types that allowed comparison of their roles in tree colonization. My previous studies (Ch. 4 & 5) suggested that *Agrostis* may inhibit *Picea* colonization. In contrast, *Picea* invasion was associated with *Anthoxanthum* (Ch. 4 & 5) and *Pteridium* (in vegetation studies of Ch. 3 & 4, but not in the edge study of Ch. 5).

Experiment 1. Competition: Effects of Sod Removal and Glyphosate Application on Seedling Emergence

Introduction

The *Agrostis* site of Field 1L (App. 3: Site 1L-AG) was chosen for an experiment in 1998 on effects of competition. It had little tree invasion and the highest grass cover (97%) among all sites examined in the 1997 vegetation survey (Ch. 4). In a prior experiment (1996-1997) in this site, plots were rototilled and seeds sown in November. The rhizomatous plant cover readily revegetated rototilled plots early in the following year, even though top growth was clipped periodically. Too few seedlings emerged for statistical analysis (however all 24 *Tsuga* and 7 *Picea* seedlings that emerged were on tilled plots, and none were on control plots). For Experiment 1 in 1L-*Agrostis*, I applied two treatments to decrease the rhizomatous layer: sod removal and application of glyphosate (Roundup®) and compared results with a control.

My hypotheses were: (1) sod removal increases seedling emergence and (2) glyphosate application increases seedling emergence.

Methods

At each of five randomly-chosen locations in the *Agrostis* meadow of Field 1L, three 1 m^2 plots were marked in similar microtopography and plant cover. Treatments were randomly assigned to the plots as follows: (1) untreated control, (2) application of glyphosate with sprouts periodically clipped, and (3) removal of the sod layer, tilling of the soil, and regrowth periodically clipped. Plots were divided into four 0.25 m^2 subplots, which were randomly assigned to *Picea*, *Tsuga*, *Alnus*, and no seeding (as a control for natural seedling emergence). Two hundred seeds were sown per subplot on 23 March 1998. Seedling emergence and survival were monitored. Logarithmic transformations [X' = log (X+1)] were applied to counts of emergent seedlings. Seedling counts were analyzed by randomized block ANOVA (mixed-model with block as random effect) followed by Bonferroni comparison of means (Statistix 2.0).

Results

Sod removal significantly increased emergence of *Picea* and of *Tsuga* (Fig. 6.2) above control plots, although emergence rates for all treatments were low and variable. Glyphosate also increased emergence but not significantly. Although glyphosate appeared to kill all above-ground plant material after application, the vegetation resprouted readily. Vegetation also steadily reoccupied the tilled plots, but at a slower rate. Thus, the degree of competition in the experimental plots increased over time. *Picea* and *Tsuga* seedlings began to appear late in May. After a July maximum, their numbers slowly declined. Most died before winter; none were found to survive the following year. Volunteer *Picea* or *Tsuga* did not occur in the unseeded field subplots.

Thus, extreme reduction of competition by sod removal increased seedling emergence of the two species (Hypothesis 1 supported). Competitor reduction by glyphosate did not increase emergence (Hypothesis 2 not supported).

Experiment 2. Competition: Effects of Competitor Reduction on Seedling Emergence and Establishment among Cover Types

Introduction

Vegetation analyses (Ch. 4) revealed that *Picea* is less likely to colonize *Agrostis* cover than *Anthoxanthum* or *Pteridium* (the edge study of Ch. 5 indicated that *Anthoxanthum* was more conducive to invasion than *Pteridium*) and suggested that *Agrostis* may provide more competition to emergent seedlings. This experiment was designed to investigate tree seedling emergence and establishment among these cover types. Two fields (2M and 3H) that have *Picea* seedlings invading along the edge were chosen. Adjacent *Pteridium* and *Agrostis* sites were present in both fields; an *Anthoxanthum* site was present only in Field 3H.

I hypothesized that: (1) competitor reduction increases seedling emergence and establishment in all three cover types and (2) competitor reduction will be more effective in increasing seedling emergence and establishment in *Pteridium* and *Anthoxanthum* than in *Agrostis* (due to sod and rhizomatous growth of *Agrostis*).

Methods

Five locations were chosen at random within each of these five sites: *Pteridium* and *Agrostis* in Field 2M and *Pteridium*, *Agrostis*, and *Anthoxanthum* in Field 3H. At each location, two 25 x 50 cm plots of similar microtopography and cover were marked and randomly assigned as either (1) control plots or (2) plots that were partially tilled. Tilling was accomplished with a tined hand-cultivator. The surface was broken in a crisscross pattern with the tines. Vegetation was periodically clipped to further reduce competitive effects. This treatment reduced competition and exposed soil, but resulted in less disturbance to the natural system than did the competitor reduction treatments in Experiment 1. It also permitted better drainage than completely tilled plots, in which rain water puddled. Seed mixtures of *Picea*, *Tsuga*, and *Alnus* (100 seeds of each species per sowing) were sown on 21-22 April and 13-14 May 1999 in each plot.

Logarithmic transformations [$X' = \log(X+1)$] were applied to counts of emergent seedlings. Emergence in early July 1999 was analyzed by a mixed-model randomized block, nested ANOVA, with site as an among-block random effect and tilling treatment as a within-block fixed effect. Analysis was by SPSS 6.1.3. Seedling numbers were too low in March 2000 for ANOVA. Seedling establishment in March was analyzed by the nonparametric Wilcoxon paired-sample test (Statistix 2.0).

To examine relationships between seedling emergence and site characteristics, I collected soil, sod, and thatch data at each of the seven sites that were examined in Experiments 1, 2, 3, and 5. Within each site, five samples were taken at the same random locations as those of the experimental blocks. Depths of thatch and sod layers were measured. Thatch is a layer of interlocking grass stems and leaves above the soil surface. Sod is a layer of surface soil held together by matted roots. Soil samples were taken at 5 to 15 cm depth during dry conditions at the end of summer. Subsamples of each of the 35 samples were oven dried at 105°C for gravimetric water content and combusted in a muffle furnace at 450°C for organic matter content (Wilde et al. 1972). Soil particle size distribution was determined by the hydrometer method after passing subsamples (air-dried and rolled) through a 2-mm sieve (Bouyoucos 1951). Differences in the soil, sod, and thatch characteristics among the seven sites were examined by Bonferroni comparison of means after one-way ANOVA.

Results

In contrast to the competitor reduction treatments of Experiment 1, partial tilling did not significantly increase the emergence of *Picea* or *Tsuga* by 8-9 July 1999 in this experiment (Table 6.2). Whereas seedling emergence in *Agrostis* control plots in Field 1L was virtually nil in Experiment 1 (Fig. 6.2), emergence in *Agrostis* in Experiment 2 was higher in control plots than tilled plots in early July (Fig. 6.3). Seedling numbers decreased more rapidly over the summer in *Agrostis* than in the other cover types. By 29-31 July 1999 the percentage of seedlings present per seeds sown decreased in *Agrostis* control plots from 1.4 % to 0.4 % for *Picea* and from 1.6 % to 0.9 % for *Tsuga*.

By March 2000, significantly more *Picea* and *Tsuga* seedlings (Wilcoxon paired-sample test: $P < 0.01$ for *Picea*, $P < 0.05$ for *Tsuga*) had established in tilled than in control plots (Fig. 6.3). These seedlings were confined to *Pteridium* and *Anthoxanthum* sites, none remained in *Agrostis* plots.

Hypotheses 1 and 2 were supported for seedling establishment in March but not for seedling emergence in the previous July. Reduction of competition by partial tilling and clipping increased seedling establishment of *Picea* and *Tsuga*, but establishment was confined to *Pteridium* and *Anthoxanthum* cover. The competitor reduction treatment did not affect seedling emergence in any cover type.

Soils were similar in texture, organic matter content, and percent moisture between adjacent *Pteridium* and *Agrostis* cover in the three experimental fields (Table 6.3), thus differences in seedling establishment between these adjacent cover types were not related to the soil characteristics. However, *Pteridium* cover had much less thatch and sod than did *Agrostis* cover in Field 3H and 1L.

The south half of Field 2M contained the five locations (2 in *Pteridium, 3* in *Agrostis*) with the highest % silt + clay among the 35 soil samples. Plots at these locations also produced the four highest seedling emergence rates among all plots of Experiments 2 & 3. This suggests that the higher moisture retention of these soils might be important to emergence.

Experiment 3. Rodent Seed Predation: Effect of Exclosures on Seedling Emergence and Establishment

Introduction

In coastal rain forests, Harmon & Franklin (1989) found that emergence of *Picea* and *Tsuga* was not affected by rodent seed predation. However, elsewhere in the Pacific Northwest, Gashwiler (1971) and Christy & Mack (1984) showed increased *Tsuga* emergence when rodents were excluded. Since seed predation by rodents also has been identified as a major inhibitor of tree colonization of eastern old fields (Myster 1993), I designed experiments to determine the effects of seed predation in the Queets fields. I chose *Pteridium* and *Agrostis* sites of a low-terrace field (1L) and of a high-terrace field (2M). Originally, I intended to use winged conifer seeds, rather than commercial wingless seeds, for all exclosure experiments to better simulate natural conditions. However, collection of sufficient seed proved difficult I also noted that, once sown in the field, seeds readily detached from wings.

Rodents generally prefer larger to smaller seeds (Muller & del Moral 1971, Reader 1997). Considering the small size of the seeds falling into dense field vegetation, I hypothesized that exclosure of rodents does not affect seedling emergence and establishment of *Picea* and *Tsuga*.

Methods

During March 1999, four locations were chosen at random in Field 1L within *Agrostis* and four within *Pteridium*, to see if seed predation was responsible for the low emergence previously noted (Experiment 1) in this field. Two similar plots at each location were randomly assigned to control or exclosure. Circular exclosures of 50-cm diameter were constructed of aluminum flashing, with 15 cm sunk below the surface and 21 cm left above. Within the exclosures, seeds were sown in an area equal to that of 25 x 50 cm control plots (1250 cm^2). A mixture of *Picea*, *Tsuga*, and *Alnus* seeds were sown on 25 March and again on 15 May. I used winged *Picea* seeds that were extracted from local cones.

This method was repeated during April 1999 in Field 2M with blocks of exclosure and control plots at five random locations in *Agrostis* and five more in *Pteridium*, except wingless seeds were used for *Picea*. (Greenhouse emergence of the winged and wingless seeds was similar.) Seeds were sown into the Field 2M plots on 22 April and again on 13 May. In addition to the exclosure experiments, an array of 16 snap traps was set to identify rodents and to provide an indication of granivore activity for two nights in Field 2M and six nights in Field 1L, during May-July 1999.

Because Experiment 3 differed between Field 1L and 2M in first sowing date and type of *Picea* seed, seedling emergence in the two fields was analyzed separately. Logarithmic transformations [$X' = \log(X+1)$] were applied to counts of emergent seedlings. Analysis (SPSS 6.1.3) was by a mixed-model randomized block, nested

ANOVA, with site (*Agrostis* or *Pteridium*) as an among-block random effect and the exclosure treatment as a within-block fixed effect.

Results

Experimental results. The exclosures did not affect seedling emergence on 8 July 1999 in Field 1L, nor was there a site effect (Table 6.4, Fig. 6.4). Emergence was low in Field 1L (~ 1% or less). In contrast, in Field 2M, seedling emergence of both *Picea* and *Tsuga* was significantly higher within the exclosures (Table 6.5). Emergence did not differ between *Pteridium* and *Agrostis* sites. More seedlings emerged in Field 2M than in 1L (Fig 6.3).

Most seedlings in either field did not survive the summer. The only seedlings remaining on 21 March 2000 were in Field 2M in one *Pteridium* exclosure (plot establishment: *Picea* = 5%, *Tsuga* 12.5%) and in one *Agrostis* control plot (*Picea* = 0.5%, *Tsuga* = 0.5%) in the heavier soils that were discussed above.

Therefore, my hypothesis that seed predation does not affect seedling emergence was supported in Field 1L, but not in Field 2M. Emergence remained low in Field 1L within exclosures. Seed predation may be important in reducing emergence of *Picea* and *Tsuga* seedlings in conditions that are otherwise beneficial to emergence.

Trapping result. During July 1999, five deer mice (*Peromyscus* spp.) were captured in 16 trap nights in *Pteridium* cover in Field 2M, within 10 m of the forest edge. None were caught in matching trap nights in adjacent *Agrostis*. During May - July 1999, no small rodents were taken in 96 trap nights in Field 1L, with traps equally divided between *Pteridium* and *Agrostis*. Runways or other signs of small rodents were not obvious on the Queets fields. Thus, *Peromyscus* may be responsible for lowering emergence in the 2M-*Pteridium* site, but did not likely play a role in Field 1L.

Experiment 4. Herbivory: Effects of Cervid Exclosures on Seedling Survival and Growth

Introduction

My permanent plot study (Ch. 3) indicated that herbivory by elk and deer suppressed growth of *Tsuga* and *Alnus* seedlings, but not of *Picea* seedlings. I designed Experiment 4 to test and quantify this effect using transplanted seedlings and cervid exclosures. I also wished to compare the effect of herbivory on seedlings with the effect of competition from herbaceous vegetation.

My hypotheses were: (1) cervid herbivory decreases survival and growth of seedlings of *Tsuga* and *Alnus*, but not *Picea*, and (2) growth of *Tsuga* and *Alnus* is depressed more by herbivory than by competition.

Methods

Two-year-old bare root seedlings of *Picea* and *Tsuga* were obtained from local nurseries. One-year *Alnus* wild seedlings were excavated from a maintenance yard of ONP. Heights of transplants averaged 38.6 ± 8.0 cm for *Picea*, 38.3 ± 8.2 cm for *Tsuga*, and 34.9 ± 10.1 cm for *Alnus*. Widths of the spreading crowns of *Tsuga* transplants averaged 38.6 ± 8.3 cm. Five locations were chosen subjectively in Fields 1L and 1M. These were widely dispersed spatially among two terraces and *Pteridium* and *Agrostis* cover. (Two locations were in 1L-*Pteridium*, one in 1L-*Agrostis*, one in 1M-*Pteridium*, and one in 1M-*Agrostis*.) This approach was taken to increase the variation among locations to enhance the generality of the hypotheses on herbivory and competition in a randomized block design.

During 21-26 March 1999, *Picea*, *Tsuga*, and *Alnus* seedlings were transplanted into blocks of three plots (1.5 x 3 m) at each location, which were randomly assigned to these treatments: (1) no treatment (control); (2) competing vegetation periodically clipped and removed; and (3) surrounded by a woven-wire fence (1.5 m tall to exclude elk and deer) and periodically clipped. Fenced exclosures were 2.5 x 4 m. Treatments of clipped versus control were designed to compare effects of different levels of competition under similar levels of herbivory. The exclosure + clipped versus clipped treatments were to examine effects of herbivory under similar levels of competition. A fourth treatment of exclosure without clipping was rejected, because I found in a preliminary experiment (not reported) that grasses grew much taller within the fences. This lush growth would introduce an increased level of competition that was not comparable to the control plots. Seedlings were transplanted in an array of three rows and eight columns, with the middle row offset such that seedlings were at least 33 cm apart. Each column contained each species, with pattern shifting regularly in adjacent columns (ABC, BCA, CAB, ABC, etc.).

Survival and height growth were monitored for one year. Relative growth rates (RGR) were used to compare growth of survivors among the treatments. RGR is defined as the change in value of a growth parameter over a time period divided by the value of the parameter at the beginning of the time period (see Ch. 3). Signs of herbivory on the transplants were noted. Maximum widths of Tsuga crowns were also measured. Survival and RGR of each species among the treatments in October 1999, after the growing season, were analyzed by randomized block ANOVA (mixed model with block as random effect) with Bonferroni comparison of means (Statistix 2.0).

Results

The exclosures did not affect survival of the two-year-old *Picea* transplanted seedlings (100% fenced plots, 98% clipped, 98% control). The exclosures also did not influence *Picea* growth rates (Fig. 6.5).

Survival of *Tsuga* decreased outside the exclosures (from 88% fenced to 65% clipped to 43% control, all differ by Bonferroni comparison at $P < 0.05$). Growth rates of *Tsuga* were significantly reduced outside the exclosures (Fig. 6.5). In contrast to *Picea* and *Alnus*, *Tsuga* was significantly browsed over winter. All surviving plants on 24 October 1999 were still alive on 21 March 2000, but their RGRs were reduced (clipped plots: mean RGR = - 9% in October to - 29% in March; control plots: - 8% to - 38%; both reductions with $P < 0.01$ by paired-*t* tests). Patterns of reduction in maximum crown widths of *Tsuga* were similar to changes in heights, though width decreased more (mean RGRs in March: clipped plots = - 61%, control plots = - 52%). Seedling crowns were trimmed by browsing into the cylindrical shape of natural browsed *Tsuga* seedlings on field edges (Ch. 3).

Alnus survival was not affected by the exclosures (83% fenced, 85% clipped, 68% control). However, *Alnus* growth was significantly higher within exclosures, where it was released from cervid herbivory (Fig. 6.5).

Competitor reduction by clipping did not increase RGRs of any of the three species compared to the control plots (Fig 6.5). However, differences in the amounts of herbaceous biomass between clipped and control plots were not large, because elk grazed both types of plots.

In accord with Hypothesis 1, cervid browsing substantially decreased net growth of the transplanted seedlings of *Tsuga* and *Alnus*, but not of *Picea*. Browsing also decreased survival of *Tsuga*, but not *Picea*. Contrary to Hypothesis 1, herbivory did not decrease survival of *Alnus*. Hypothesis 2 was supported, as competitor reduction by clipping had no effect on net growth of any species, hence was less important than herbivory for *Tsuga* and *Alnus*. While competitor reduction treatments did show effects on emergent seedlings in Experiments 1 and 2, the larger seedlings in Experiment 4 may be less vulnerable to these treatments.

Experiment 5: Effect of Plant Cover on Seedling Survival and Growth

Introduction

In Experiment 4, I used exclosures to examine the direct effects of cervid herbivory on three species of transplanted seedlings. In Experiment 5, I examined if herbivory effects varied among sites. My aerial photographic analysis (Ch. 3) and vegetation analyses (Ch. 4) suggested a positive association between *Pteridium* cover and *Picea* invasion. Thus, sites also were chosen to investigate possible facilitation of *Picea* by *Pteridium*.

For this experiment, I hypothesized that (1) cervid browsing is greater on *Tsuga* and *Alnus* than *Picea*, which leads to greater survival and growth of *Picea* seedlings, and (2) growth rate of *Picea* is greater in two *Pteridium* sites than in two adjacent grass-dominated sites.

Methods

The same stocks of *Picea*, *Tsuga*, and *Alnus* seedlings described above in Experiment 4 were used for this experiment. During 23-24 March 1999, I transplanted seedlings into arrays at five random locations within four sites: (1) Field 2M *Pteridium*, (2) adjacent *Agrostis*, (3) Field 3H *Pteridium*, and (4) adjacent *Anthoxanthum*. The seedlings were transplanted in rectangular arrays (1 x 2.5 m) of 3 rows and 5 columns at each location, with plants 50 cm apart. Each column contained each species, with pattern shifting regularly in adjacent columns (ABC, BCA, CAB, ABC, etc.). Signs of herbivory were recorded periodically throughout the year. Seedling growth and survival were measured on 23-24 October 1999.

Survival among the three species was analyzed by randomized block ANOVA with Bonferroni comparison of means. Too few *Tsuga* and *Alnus* survived to compare growth rates among the species. *Picea* growth rates in the two *Pteridium* sites were compared to the two grass-dominated sites by the Scheffe test for multiple contrasts (Zar 1996), after one-way ANOVA of the four sites.

Results

There was no significant difference in *Picea* seedling survival among the four sites (92% overall). *Picea* seedling survival was significantly higher than either *Tsuga* (32%) or *Alnus* (17%) in October 1999 ($P < 0.05$, Bonferroni comparisons after randomized block ANOVA). Nearly all *Tsuga* seedlings that died, in both Experiments 4 and 5, were either partially or totally pulled out of the ground within a month of transplanting.

Relative growth rates for *Picea* on 23-24 October 1999 (Fig. 6.6) were significantly higher ($P < 0.05$ by the Scheffe multiple contrast test) in the two *Pteridium* sites (31% in 3H-PA, 30% in 2M-PA) than in the two grass-dominated sites (11% in 3H-AO, 7% in 2M-AG).

Results of this experiment supported both of my hypotheses. Browsing suppressed *Tsuga* and *Alnus* but not *Picea*. Growth of *Picea* was greater in *Pteridium* than adjacent grass-dominated areas. Growth did not differ between the *Anthoxanthum* and *Agrostis* sites, which is notable because *Anthoxanthum* is more conducive to *Picea* invasion than *Agrostis* (Ch. 4 & 5 & Experiment 2 in this chapter).

Discussion

Competition

Reduced competition increased seedling establishment of *Picea* and *Tsuga* in *Pteridium* and *Anthoxanthum* sites (Experiment 2). Even though seedlings emerged in *Agrostis* at rates comparable to those in *Pteridium* or *Anthoxanthum*, survival in *Agrostis* was lower. In the low-terrace *Agrostis* site (Experiment 1), emergence was low regardless of treatment. Emergence was increased only by sod removal, which indicates that the sod layer associated with *Agrostis* is important in competition. These results were consistent with my proposal in Chapters 4 and 5 that competition with field vegetation is a major barrier to tree seedling colonization and that this competition is more severe in sites dominated by *Agrostis*.

In Pacific Northwest temperate rain forests, Harmon and Franklin (1989) concluded that *Picea* and *Tsuga* regeneration is essentially excluded from the forest floor by competition from herbs and mosses. Thus, it is not surprising that these small-seeded species would have difficulty establishing in the lush herbaceous cover of the old fields. In a similar situation, Prach et al. (1996) found that competition by dense cover in a 50-

year old field dominated by the sodgrass *Holcus mollis* inhibited invasion by *Picea abies*. *Alnus*, with smaller seeds and regeneration adapted to open mineral soil (Fowells 1965), is even less suited to establishment in the fields, as illustrated by the almost total lack of emergence in my experiments.

Most *Picea* and *Tsuga* seedlings did not emerge in the Queets fields until July, when conditions were dry. In fact, the summers of 1998 and 1999 were drier than normal (App. 1). Emergence in the 1999 experiments was highest in plots in Field 2M that had the highest percentage of silt and clay. Moisture retention by the heavier soils may have promoted germination and emergence. Emergence was least in Field 1L, which had lower moisture retention from sandy soils and less organic matter. *Picea* and *Tsuga* germinants grow slowly and are susceptible to moisture stress (Gaswhiler 1971, Schopmeyer 1974, Gray & Spies 1997).

Cervid herbivory

Cervid herbivory does not affect *Picea* but presents a second hurdle to *Tsuga* and *Alnus* seedlings that manage to overcome the formidable barriers to seedling emergence. Within exclosures, *Tsuga* transplants grew at a rate similar to *Picea*, but outside the fences, they suffered a net decrease in survival, height, and crown width during the growing season, and a further decrease in size over winter. In regional rain forests, elk browse readily on *Tsuga*, particularly in winter (Leslie et al. 1984) and are thought to decrease *Tsuga* regeneration relative to *Picea* (Woodward et al. 1994). In other regions, cervid herbivory has been implicated in the differential ability of tree species to colonize old fields (De Steven 1991b, Hill et al. 1995, Lawson et al. 1999). Suppression of *Tsuga* and *Alnus* growth by herbivory in my transplant experiments paralleled results of my permanent-plot study of natural seedling growth (Ch. 3). My exclosure experiment demonstrated the rapid growth potential of *Alnus* in the fields, if it were able to emerge and avoid herbivory.

Rodent seed predation

My results suggested that rodent seed predation may decrease seedling emergence in some sites but not others (Experiment 3). Exclosures had the strongest effect in Field 2M *Pteridium*, in an area with demonstrated *Peromyscus* activity. *Peromyscus* are known to consume *Picea* and *Tsuga* seeds (Gaswhiler 1967, Maser et al. 1981) and probably decrease emergence of seedlings in the Queets fields where they occur. The exclosures had no effect on the low-terrace Field 1L, where experimental emergence was generally low. *Peromyscus*, which are highly trappable (Verts & Carraway 1998), were not captured in *Pteridium* in Field 1L, despite intensive effort compared to Field 2M. It is possible that the results of exclosure experiments reflect not only seed predation, but also predation on newly-emergent seedlings that occurred before I noted their presence. *Microtus* are well-known herbivores in old fields (Gill & Marks 1991, Ostfield & Canham 1993), but were not trapped in my study, nor were any signs of their presence obvious.

My results are inconclusive on the role of rodents in inhibition of tree seedling colonization of the Queets fields. Availability of suitable microsites with low competition may be more important than rodent seed predation. *Picea* and *Tsuga* seedlings are most abundant in certain field edges, even though *Peromyscus* is also more likely to frequent the edges of fields (Ostfield et al. 1997, Meiners 1999). In coastal forests, Harmon and Franklin (1989) found seed predation insignificant in emergence of *Picea* or *Tsuga*, although elsewhere in the Pacific Northwest, Gashwiler (1971) and Christy and Mack (1984) found greater emergence of *Tsuga* seedlings when rodents were excluded. Harmon and Franklin argued that the massive quantity of *Picea* or *Tsuga* seed produced in good years would outweigh even high seed predation.

Facilitation by Pteridium

Results of Experiment 5 support the hypothesis that *Pteridium* facilitates growth of *Picea* in the fields. However, my study does not demonstrate whether *Picea* is directly facilitated by *Pteridium*, or indirectly benefits from another factor associated with *Pteridium*. My study of *Picea* edge invasion (Ch. 5) suggested that the grass cover beneath *Pteridium*, and not *Pteridium* cover itself, was an important factor. In Experiment 5, though, *Picea* grew just as effectively in *Pteridium-Agrostis* as in *Pteridium-Anthoxanthum* (Fig 6.6). Berkowitz et al. (1995) reported facilitation of tree seedlings by old-field vegetation during drought stress. *Picea* seedlings may fare better in *Pteridium* due to a decrease of moisture stress by summer shading, but shading experiments are needed to verify this.

Summary

These experiments demonstrated that the primary inhibition of tree colonization of the Queets old fields is the failure of seedlings to establish from seed. In Experiments 1-3, few seeds became seedlings, and very few of these seedlings survived a full year, regardless of treatment. The experiments suggest that this difficulty in establishment is due to competition. This competition occurs within a framework of limited summer moisture.

The effects of competition, herbivory, and seed predation on seedling establishment and growth varied among sites in my study. This underscores the importance of researchers replicating experiments across a range of conditions before generalizing about the mechanisms of succession.

Table 6.1. Guide to experiments: mechanisms tested, manipulations (= treatments other than controls), and locations. Site characteristics in App. 3. Site code: PA = *Pteridium*, AG = *Agrostis*, AO = *Anthoxanthum*.

			sites of experiment						
Ex. #	mechanisms	manipulations	1L-PA	1L-AG	2M-PA	2M-AG	3H-PA	3H-AG	3H-AO
seed sowing									
1	competition	desodded/tilled, clipped		X					
		glyphosate, clipped		X					
2	competition	partially-tilled, clipped			X	X	X	X	X
3	seed predation	aluminum flashing exclosures	X	X	X	X			
seedling transplants									
4	herbivory, competition	fence exclosures, clipped	X	X					
		clipped	X	X					
5	herbivory, facilitation	(none - different sites)			X	X	X		X

Table 6.2. ANOVA for *Picea* and *Tsuga* seedling emergence in Field 2M and 3H on 8-9 July 1999 in Experiment 2. Site (S) = 2M-*Pteridium*, 2M-*Agrostis*, 3H-*Pteridium*, 3H-*Agrostis*, or 3H-*Anthoxanthum*. Till treatment (T) = tilled or control. Counts were log-tranformed. B/S = blocks within site. No effects were significant at P < 0.05.

	SOURCE	df	MS	F	P
Picea	between blocks				
	Site (S)	4	.14	1.26	.32
	error: B/S	20	.11		
	within blocks				
	Till (T)	1	.07	.94	.69
	S x T	4	.04	.57	.35
	error: T x B/S	20	.07		
Tsuga	between blocks				
	Site (S)	4	.16	1.08	.39
	error: B/S	20	.15		
	within blocks				
	Till (T)	1	.03	.49	.49
	S x T	4	.12	2.05	.13
	error: T x B/S	20	.06		

Table 6.3. Mean values of selected characteristics of sites of Experiments 1, 2, 3, and 5. Different superscript letters indicate means differ by $P < 0.05$ by Bonferroni comparison after one-way ANOVA of the seven sites. Superscripts alphabetized from high to low values. Cover type code: PA = *Pteridium*, AG = *Agrostis*, AO = *Anthoxanthum*. Fields arranged from low to high terrace soils. Each of the sites had 5 randomly-located samples.

	Sites						
	1L-PA	1L-AG	2M-PA	2M-AG	3H-PA	3H-AG	3H-AO
soil characteristic							
% silt	36^{cd}	29^{de}	49^{ab}	56^{a}	44^{bc}	37^{cd}	23^{e}
% clay	3^{c}	3^{c}	6^{abc}	9^{a}	8^{a}	6^{ab}	4^{bc}
% organic matter	7.7^{d}	6.4^{d}	10.5^{bc}	9.9^{c}	11.7^{ab}	12.7^{a}	11.8^{ab}
% water	21.1^{bc}	21.5^{bc}	39^{a}	37^{a}	37^{a}	30^{ab}	18^{c}
sod and thatch							
cm sod	0.4^{d}	3.5^{ab}	2.1^{bc}	2.8^{ab}	0.8^{cd}	4.2^{a}	3.0^{ab}
cm thatch	1.2^{c}	4.4^{a}	2.6^{abc}	1.5^{bc}	1.2^{c}	3.2^{ab}	1.4^{bc}

Table 6.4. ANOVA for *Picea* and *Tsuga* seedling emergence in Field 1L on 8 July 1999 in Experiment 3. Site (S) = *Pteridium* or *Agrostis*. Exclosure treatment (E) = exclosure or control. B/S = blocks within site. Counts were log-transformed. No effects were significant at $P < 0.05$.

	SOURCE	df	MS	F	P
Picea	between blocks				
	Site (S)	1	.01	.13	.73
	error: B/S	6	.05		
	within blocks				
	Exclosure (E)	1	.02	.16	.71
	S x E	1	.00	.01	.93
	error: E x B/S	6	.13		
Tsuga	between blocks				
	Site (S)	1	.04	.36	.57
	error: B/S	6	.12		
	within blocks				
	Exclosure (E)	1	.09	2.28	.18
	S x E	1	.16	4.13	.09
	error: E x B/S	6	.04		

Table 6.5. ANOVA for *Picea* and *Tsuga* seedling emergence in Field 2M on 8 July 1999 in Experiment 3. Site (S) = *Pteridium* or *Agrostis*. Exclosure treatment (E) = exclosure or control. B/S = blocks within site. * = P < 0.05, ** = P < 0.01. Counts were log-transformed.

	SOURCE	df	MS	F	P
Picea	<u>between blocks</u>				
	Site (S)	1	.24	1.07	.33
	error: B/S	8	.23		
	<u>within blocks</u>				
	Exclosure (E)	1	2.69	40.30	**<.01
	S x E	1	.28	4.21	.07
	error: E x B/S	8	.07		
Tsuga	<u>between blocks</u>				
	Site (S)	1	.09	.49	.51
	error: B/S	8	.18		
	<u>within blocks</u>				
	Exclosure (E)	1	.93	6.32	*.04
	S x E	1	.07	.47	.51
	error: E x B/S	8	.15		

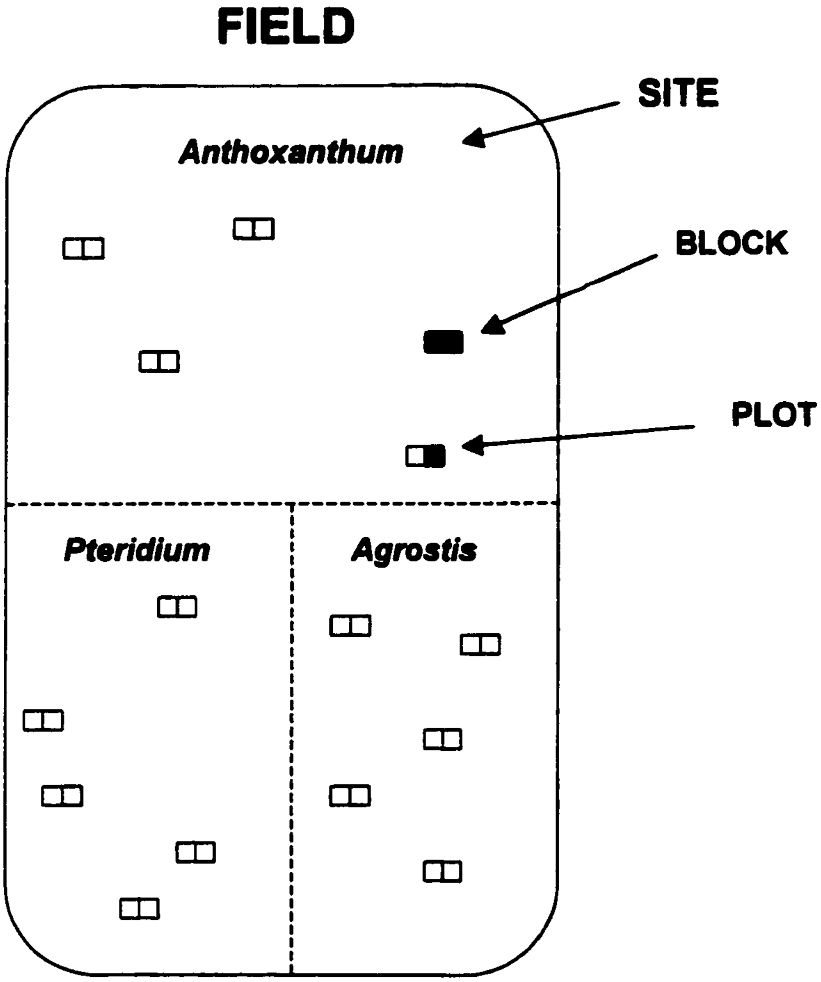

Figure 6.1. Sampling scheme for most experiments, with terminology. Fields were divided into sites (dashed lines) as described in Ch. 4, named by dominant cover type (*Agrostis*, etc.). Five blocks of plots were randomly located within sites. Treatments were randomly assigned to plots within the blocks.

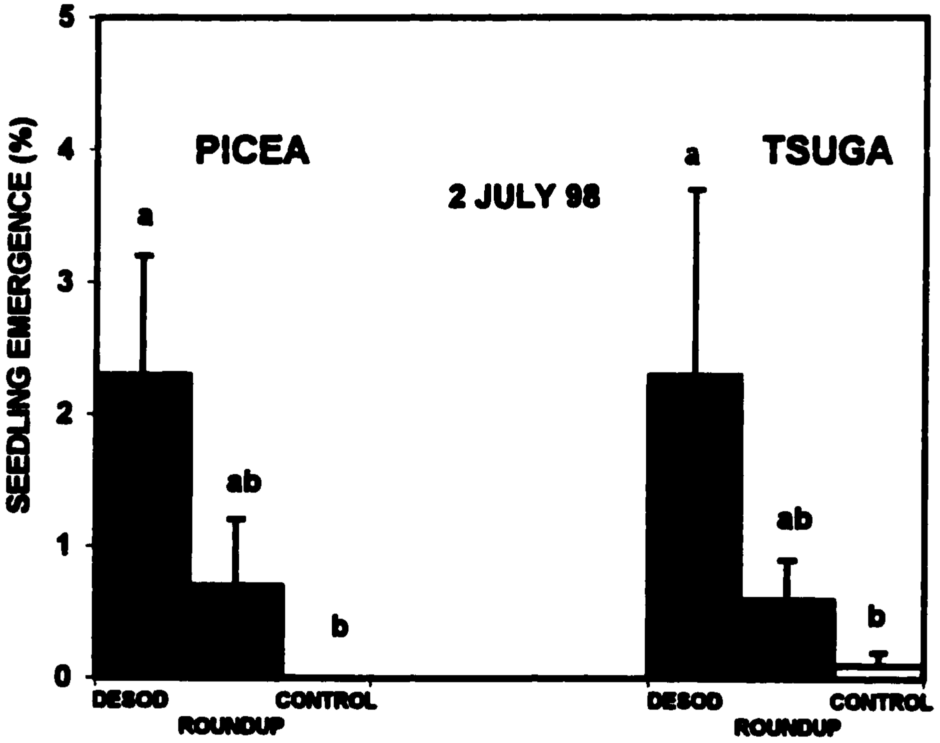

Figure 6.2. Mean (+SE) percent seedling emergence of *Picea* and *Tsuga* in Experiment 1 in Field 1L *Agrostis*. In treatment contrasts of desodded (dark shaded), glyphosate (Roundup = gray shaded), and control (unshaded), different letters indicate means differ by $P < 0.05$ by Bonferroni comparison after randomized block ANOVA. Comparisons were on log transformed counts.

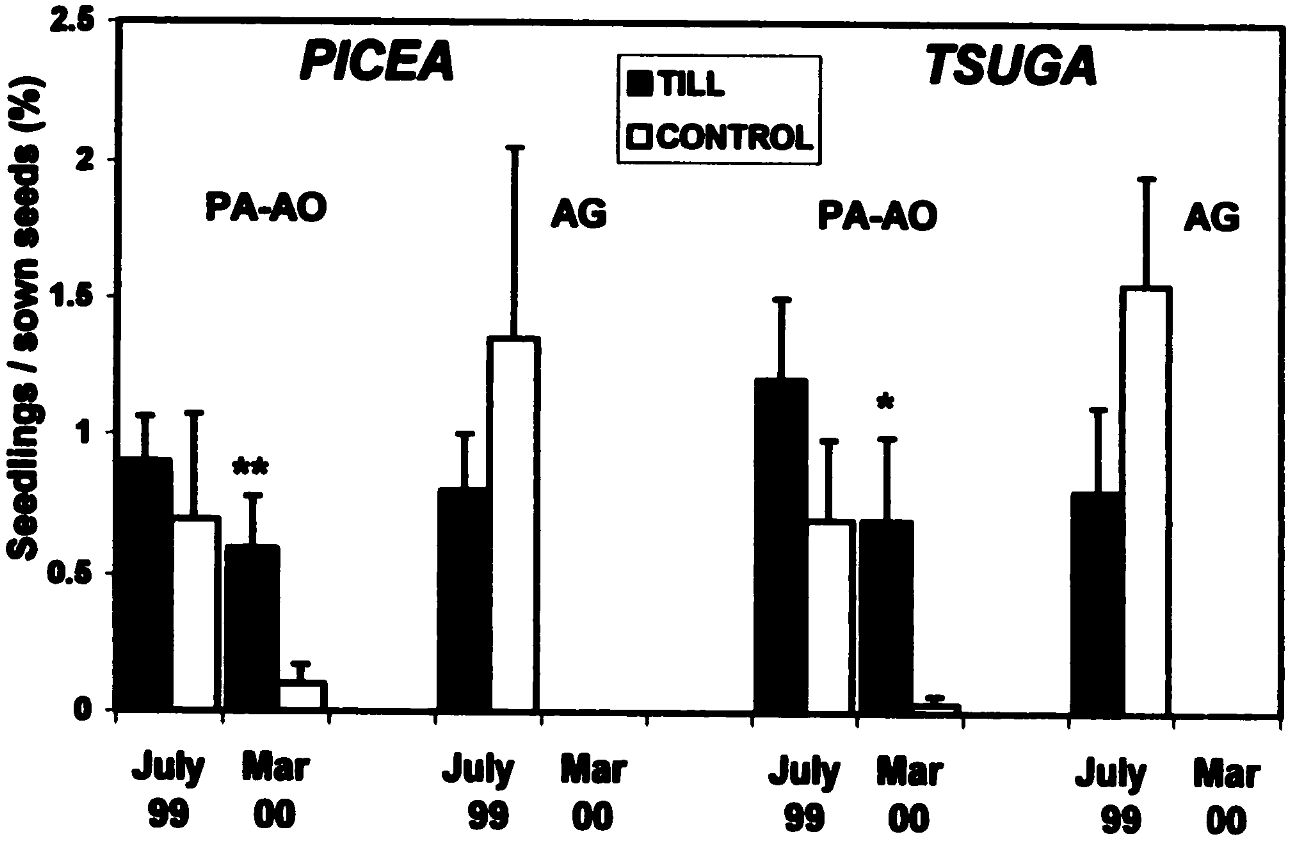

Figure 6.3. Mean (+SE) percent seedling emergence on 8-9 July 1999 and seedling establishment on 20 March 2000 of *Picea* and *Tsuga* in Experiment 2. Graph compares *Agrostis* (AG) sites to *Pteridium* (PA) & *Anthoxanthum* (AO) sites. Mean emergence in July 1999 of sites did not differ by split-plot ANOVA (Table 6.2). * $P < 0.05$, ** $P < 0.01$ that means of tilled vs. control plots differ by Wilcoxon paired-sample test (data too few for ANOVA in March 2000). No seedlings remained in *Agrostis* plots in March 2000. Comparisons were on log transformed counts.

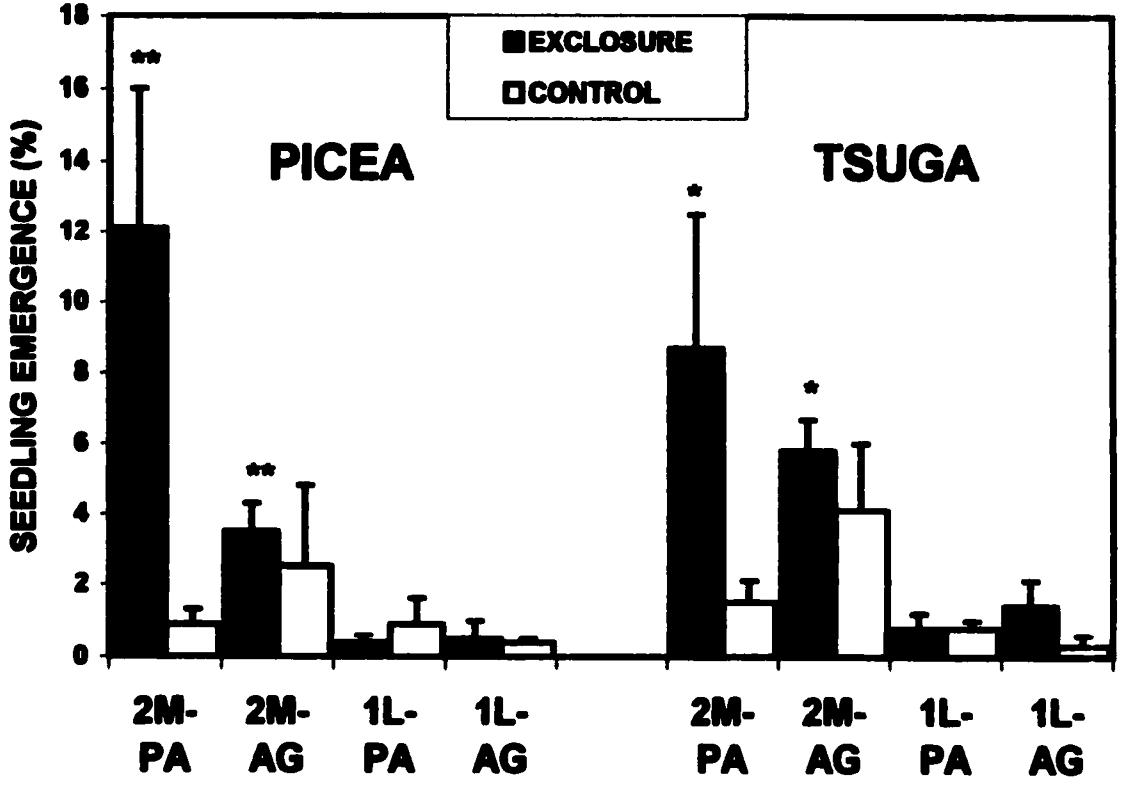

Figure 6.4. Mean (+SE) percent seedling emergence of *Picea* and *Tsuga* in Experiment 3 in Fields 2M & 1L for 8 July. Exclosures increased emergence of both species in Field 2M (Table 6.5) but not 1L (Table 6.4). Cover type code: PA = *Pteridium*, AG = *Agrostis*. *$P < 0.05$, **$P < 0.01$ that means of exclosure vs. control plots differ by ANOVA (Table 6.5).

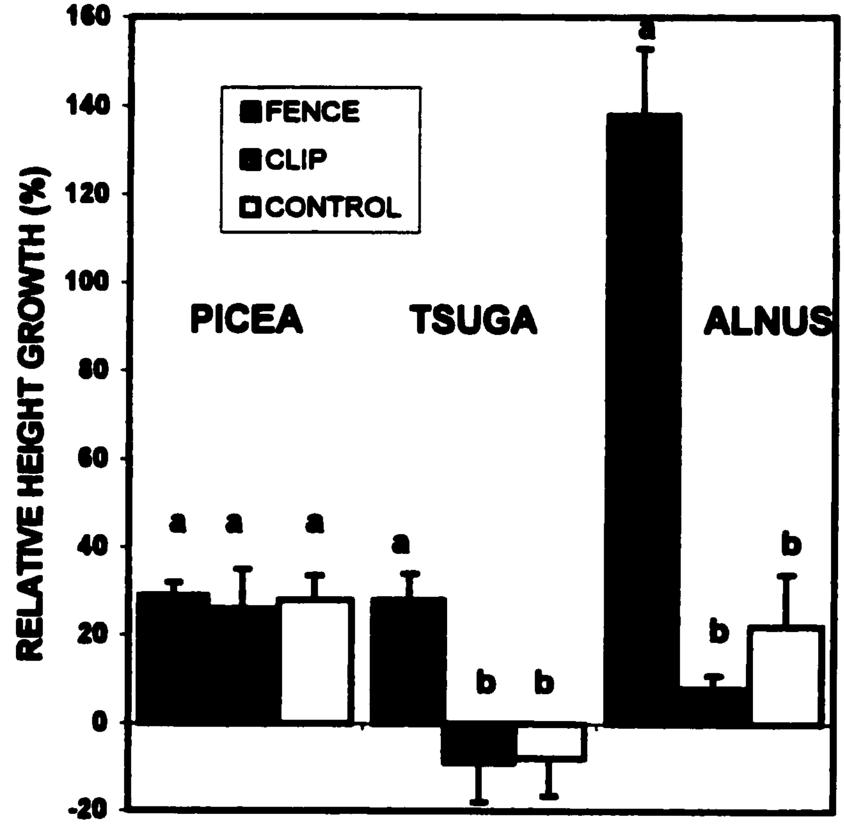

Figure 6.5. Mean (+SE) percent relative growth rates (RGRs) in height of transplanted seedlings of *Picea*, *Tsuga*, and *Alnus* in Experiment 4, planted 21-26 March 1999 and measured 24 October 1999. Treatments: FENCE = within fenced exclosures + clipped; CLIP = outside exclosures + clipped; CONTROL = outside exclosure, no clipping. Within each species, different letters indicate means differ by $P < 0.05$ by Bonferroni comparison after randomized block ANOVA.

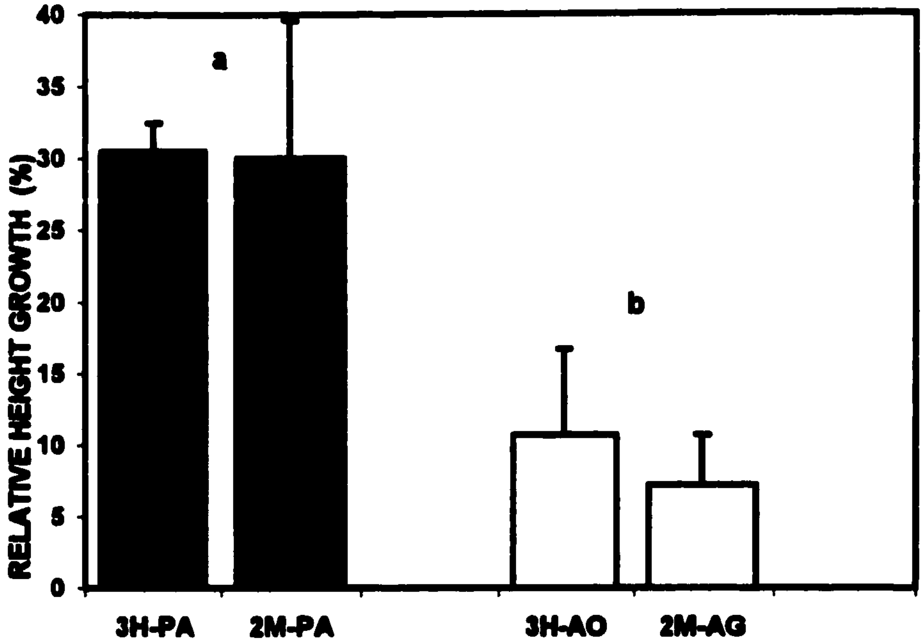

Figure 6.6. Mean (+SE) percent relative growth rates (RGRs) in height of transplanted seedlings of *Picea* among sites in Experiment 5 in Fields 3H and 2M. Seedlings were planted 23-24 March 1999 and measured 23-24 October 1999. Different letters indicate that means of *Pteridium* sites (shaded) and grass-dominated sites (unshaded) differ by P < 0.05 by the Scheffe multiple contrast test after one-way ANOVA of the 4 sites. Cover types: PA = *Pteridium*, AO = *Anthoxanthum*, AG = *Agrostis*.

7. INTEGRATION

Summary of chapter studies

The dominant trees of the surrounding forests, ***Picea sitchensis*, *Tsuga heterophylla***, and ***Alnus rubra***, rarely establish on the abandoned Queets fields (Ch. 4), primarily because of competition from field vegetation (Ch. 5 & 6). Tree colonization is rare in plant cover dominated by *Agrostis gigantea*, *Carex obnupta*, *Cirsium arvense*, or *Rubus laciniatus*. *Picea*, the most successful invader, is essentially confined to areas dominated by *Anthoxanthum odoratum* or *Pteridium aquilinum* on the edges of fields on higher alluvial terraces (Ch. 4). In experiments with sown seeds, seedlings of *Picea* or *Tsuga* emerged as readily in *Agrostis* as in *Pteridium* or *Anthoxanthum*, but there they suffered higher mortality (Ch. 6), perhaps due to increased competition by *Agrostis* and its rhizomatous associates. Even in *Pteridium* or *Anthoxanthum*, establishment was rare without experimental reduction of competing surface vegetation. *Picea* invasion along field edges was associated with a lack of *Agrostis* cover, with attendant lessening of sod thickness and ground cover (Ch. 5). Soil organic matter and moisture retention may also benefit *Picea* invasion.

Seed predation by rodents appeared to reduce the number of seedlings emerging in some areas but not others. Effects of rodent seed and seedling predation warrant further investigation but may not be critical to tree colonization. *Tsuga* and *Alnus* seedlings that do emerge on the fields are suppressed by cervid herbivory (Ch. 3 & 6). In contrast, once *Picea* seedlings establish, they grow steadily and suffer little mortality from browsing (Ch. 3). Growth of *Picea* seedlings may be facilitated by *Pteridium* (Ch. 6).

Effects of barriers to sapling establishment of *Picea* and *Tsuga* for three types of sites are summarized in Fig 7.1. Percent survival of plants for each barrier is estimated from experimental and permanent-plot data. Dispersal of the small *Picea* and *Tsuga* seeds is not considered an important barrier to establishment (Ch. 3). However, seedfall decreases with distance from field edges. Thus, in my flow chart, more seeds falling on edges would result in more seedlings, in pathways where seedlings survive.

Seedling emergence without and with rodent predation is estimated in Fig. 7.1 from results of Experiment 3 (Ch. 6). If rodent predation were absent in *Pteridium* or *Anthoxanthum* on high-terrace soils, *Picea* establishment might increase tenfold (9 saplings per 1000 seeds, according to the model). This suggests that rodents may be an effective inhibitor in areas where more seedlings otherwise emerge (it is possible that the rodents consumed newly-emergent seedlings, as well as seeds; see Ch. 6).

Establishment of seedlings was estimated from results from control plots for Experiment 2 in March 2000. Survival of seedlings < 10 cm tall and growth of saplings to > 2 m tall were estimated from permanent-plot data (Ch. 3).

As Fig. 7.1 illustrates, sapling colonization is almost completely limited to *Picea* in high-terrace *Anthoxanthum* or *Pteridium* cover.

Restoration to forest - management recommendations

If the goal of park managers is to replace exotic old-field vegetation with native species, my experiments suggest that transplanting of *Picea* seedlings into existing cover would be most effective. Initial growth should be better in *Pteridium* areas, but *Picea* transplants also grow in *Agrostis*. Site preparation by tilling or mowing is not recommended before transplanting, because herbaceous cover may benefit *Picea* growth by partial shading during the dry summer.

Establishment of *Picea* by seed is impractical and was almost nonexistent in my experiments, regardless of treatment. I also conducted experiments on seedling emergence of *Picea* and *Tsuga* on logs transported into the fields (unreported data). Use of nurse logs to facilitate emergence is problematic, because log surfaces face desiccation in the open fields during the dry summers. Results might be improved by use of large logs, logs with a thin moss layer, logs with established seedlings, and placement in shaded areas. Large logs arrayed in a "jam" that protected inner logs from elk herbivory may also promote *Tsuga* establishment (by creating refugia, Schreiner et al. 1996).

My results showed the rapid growth potential of *Alnus* on low-terrace soils if protected from herbivory. If transplanted *Alnus* seedlings were protected, *Alnus* would grow more rapidly into a mature stand than would *Picea*. However, if the concern of park managers is to remove nonnative species, exotic ground cover is more likely to persist under *Alnus* than under *Picea*. Herbaceous cover in riparian *Alnus* forests in Olympic National Park is usually dominated by nonnative species (Fonda 1974, DeFerrari & Naiman 1994). Direct establishment of *Picea* forest would most efficiently create understory conditions that replace the exotic species with native plants (Ch. 4).

Future studies

My study indicated that the intensities of processes important to tree colonization (competition, seed predation, facilitation) varied among the different plant communities (*Agrostis*, *Anthoxanthum*, *Pteridium*). I suggested reasons for this variation from my data, but I believe that experimental investigation at the microsite level of a system such as this is a logical next step in our understanding of old field succession. Seeds could be sown in small plots in different plant communities, under appropriate treatments of competitor (or facilitator) removal and animal exclosure. Emergent seedlings would be marked and their fates closely monitored. Microsite conditions of moisture, light, temperature, and soil properties would be measured and manipulated. The potential roles of mycorrhizae or allelopathy on seedling establishment, which were not examined in my study, might be investigated at this level. However, my study suggested that competition is the most important limiting factor. Thus, a microsite investigation of the mechanics of competition between trees and field herbs merits first attention.

Old field studies have come a long way in elucidating the mechanisms affecting succession. But it may be time to get down in the dirt with micro-scale tools, to see the world from the view of a seed or seedling.

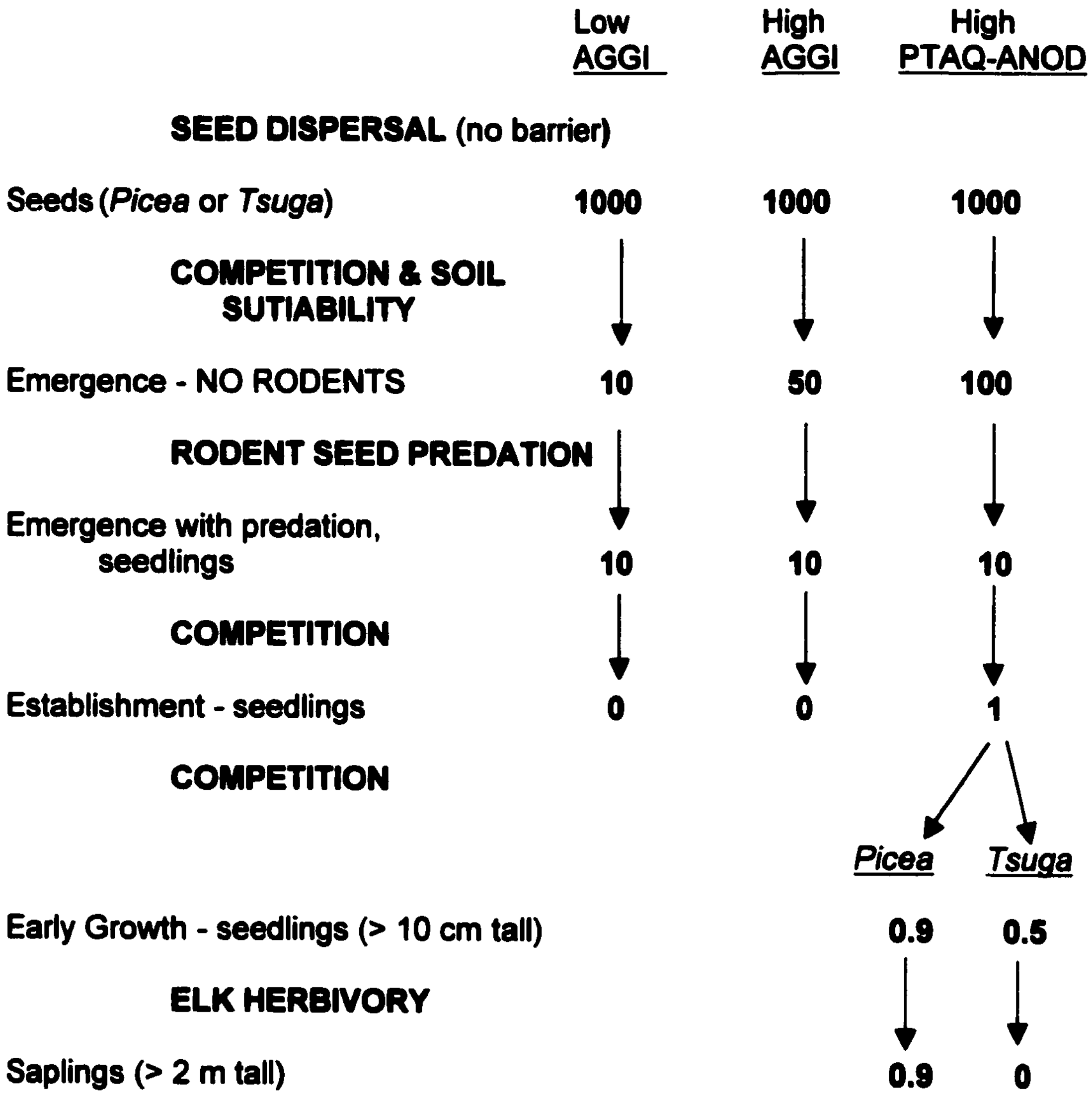

Figure 7.1. Summary flow chart of effects of barriers (in bold capitals) on sapling establishment of *Picea* and *Tsuga*. Number of surviving individuals from 1000 original seeds are estimated after each barrier for three types of fields: low terrace *Agrostis* (AGGI), high-terrace *Agrostis*, and high terrace *Pteridium* (PTAQ) or *Anthoxanthum* (ANOD). Estimates are from results of experiments and permanent-plot studies, as explained in text.

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Appendix 1. Monthly weather records, Clearwater, Washington, 1996-1999.

temperature (^{o}C)	normal	1996	1997	1998	1999
January	4.3	4.8	5.4	5.6	5.2
February	6.0	5.7	5.8	6.7	8.3
March	6.9	7.6	6.6	7.8	5.8
April	8.6	9.9	9.0	8.4	7.8
May	11.1	10.4	13.1	12.0	9.7
June	13.4	13.2	14.1	13.9	12.8
July	15.2	16.3	15.7	16.7	14.8
August	15.6	15.9	17.1	15.7	15.8
September	15.4	13.1	15.9	13.9	14.8
October	10.8	9.7	11.3	10.7	11.1
November	6.9	6.2	8.4	7.9	7.8
December	4.6	3.9	5.2	3.9	
precipitation (cm)					
January	41.8	38.3	53.2	45.6	43.8
February	36.4	28.6	24.1	34.2	63.6
March	33.0	12.6	48.1	24.4	37.6
April	22.0	34.9	28.7	7.3	11.1
May	15.4	12.0	20.5	12.2	15.4
June	8.6	5.6	20.4	4.5	10.1
July	7.3	2.9	10.7	7.9	3.5
August	7.7	7.1	13.0	0.0	7.5
September	15.4	10.5	34.2	1.2	3.6
October	29.4	42.6	37.8	19.1	29.3
November	42.7	35.1	31.6	61.1	47.2
December	45.1	48.1	29.6	64.5	

Appendix 2. Species encountered in 1997 Field Survey and 1999 Edge Study

	Native (N) or Exotic (E)	1997 Field Survey	1999 Edge Study
Grasses			
Agrostis capillaris	E	X	
Agrostis gigantea	E	X	X
Anthoxanthum odoratum	E	X	X
Cynosurus cristatus	E	X	
Dactylis glomerata	E	X	X
Elytrigia repens	E	X	
Festuca pratensis	E	X	
Holcus lanatus	E	X	X
Holcus mollis	E	X	
Lolium perenne	E	X	
Phalaris arundinacea	E	X	
Poa pratensis	E	X	X
Poa trivialis	E	X	
Sedges & Rushes			
Carex obnupta	N	X	X
Juncus bufonius	E	X	
Juncus effusius	N	X	
Forbs			
Achillea millefolium	E	X	X
Cerastium arvense	E	X	X
Chrysanthmum leucanthemum	E	X	X
Cirsium arvense	E	X	X
Cirsium vulgare	E	X	X
Crepis capillaris	E	X	X
Equisetum arvense	N	X	
Hypochaeris radicata	E	X	X
Lotus micranthus	E	X	
Mentha arvensis	E	X	
Plantago lanceolata	E	X	X
Prunella vulgaris	E	X	X
Ranunculus repens	E	X	X
Rumex acetosella	E	X	X
Rumex obtusifolius	E	X	
Senecio jacobea	E	X	

Appendix 2 (continued)

	Native (N) or Exotic (E)	1997 Field Survey	1999 Edge Study
Taraxacum officinale	E	X	
Trifolium dubium	E	X	
Trifolium repens	E	X	X
Veronica officinale	E	X	
Veronica serpyllifolia	E	X	X
<u>Forest herbs</u>			
Claytonia siberica	N	X	
Fragaria virginiana	N	X	X
Galium triflorum	N	X	X
Mainthemum dilatum	N	X	X
Oxalis oregona	N	X	X
Spiranthes romanzoffiana	N		X
Stachys cooleyae	N	X	X
Tiarella trifoliata	N	X	X
Tolmiea menziesii	N	X	
<u>Ferns</u>			
Blechnum spicant	N		X
Polystichum munitum	N	X	X
Pteridium aquilinum	N	X	X
<u>Mosses & Liverworts</u>			
Conocephalum conicum	N		X
Hylocomium splendens	N		X
Polytrichum juniperinum	N		X
Rhytidiadelphus loreus	N		X
<u>Lichen</u>			
Peltigera neopolydactyla	N		X
<u>Shrubs</u>			
Rubus discolor	E	X	
Rubus laciniatus	E	X	X
Rubus spectabilis	N	X	
Rubus ursinus	N	X	
Sambucus racemosa	N	X	
Vaccinium parvifolium	N	X	

Appendix 2 (continued)

	Native (N) or Exotic (E)	1997 Field Survey	1999 Edge Study
Trees			
Acer circinatum	N	X	
Acer macrophyllum	N	X	
Alnus rubra	N	X	X
Frangula purshiana	N	X	X
Oemleria cerasiformis	N	X	
Picea sitchensis	N	X	X
Prunus cerasus	E	X	
Pyrus fusca	N	X	X
Pyrus malus	E	X	
Salix scouleriana	N	X	
Tsuga heterophylla	N	X	X

Appendix 3. Site values for environmental variables and percent cover of major species.

	<u>Site</u>					
	1L-PA	1L-AG	2L-RL	2L-AG	2M-PS	2M-PA
soil % organic matter	5.5	5.1	6.1	5.1	8.0	9.2
soil % water	32	31	43	30	44	45
soil pH	4.1	4.1	4.3	4.2	4.1	4.2
soil % sand	61	66	35	46	39	43
AI - agricultural intensity	3	3	2	3	1	2
burning before clearing	2	2	3	3	3	3
<u>% cover</u>						
Agrostis gigantea	31	60	25	49	9	46
Anthoxanthum odoratum	3	6	3	1	7	2
Holcus lanatus	25	15	21	33	2	12
Holcus mollis	0	0	0	0	0	0
Carex obnupta	0	0	0	0	6	21
Cirsium arvense	0	0	4	12	0	2
Hypochaeris radicata	6	4	0	0	3	0
Plantago lanceolata	6	2	1	2	2	2
Ranunculus repens	13	26	17	2	3	5
Trifolium repens	18	8	10	18	0	5
Pteridium aquilinum	49	1	26	0	37	62
Rubus laciniatus	12	1	48	0	2	8
Rubus ursinus	6	0	0	0	9	1
Alnus rubra	0	0	1	0	11	0
Frangula purshiana	0	0	1	0	7	0
Picea sitchensis	0	0	0	0	57	0
Tsuga heterophylla	0	0	0	0	3	0

Appendix 3. (continued)

	Site					
	2M-AG	2H-PS	2H-AG	3L-CO	3L-AG	3H-AO
soil % organic matter	7.6	9.0	8.9	5.5	5.9	6.8
soil % water	45	46	46	38	35	31
soil pH	4.3	4.1	4.0	4.3	4.2	4.1
soil % sand	35	50	47	50	44	62
AI - agricultural intensity	3	1	2	2	2	2
burning before clearing	3	3	3	3	3	3
% cover						
Agrostis gigantea	63	11	51	14	39	37
Anthoxanthum odoratum	4	6	14	10	11	49
Holcus lanatus	15	5	14	5	22	0
Holcus mollis	0	0	0	0	0	0
Carex obnupta	9	7	2	67	11	4
Cirsium arvense	1	0	0	5	22	0
Hypochaeris radicata	1	1	1	5	4	6
Plantago lanceolata	1	3	1	2	2	12
Ranunculus repens	8	7	16	3	5	4
Trifolium repens	5	0	7	7	13	0
Pteridium aquilinum	11	51	35	10	3	23
Rubus laciniatus	6	7	13	13	12	1
Rubus ursinus	0	21	2	11	2	0
Alnus rubra	0	11	0	0	0	0
Frangula purshiana	0	9	1	3	0	0
Picea sitchensis	0	48	2	0	3	1
Tsuga heterophylla	0	1	0	0	0	0

Appendix 3. (continued)

	Site					
	3H-PA	3H-AG	4H-PS	4H-AO	5L-AG	6L-AG
soil % organic matter	10.2	10.3	7.8	11.2	5.4	2.3
soil % water	47	42	46	38	27	26
soil pH	4.0	4.2	4.0	4.2	4.3	4.4
soil % sand	57	53	54	58	65	50
AI - agricultural intensity	2	2	2	2	3	3
burning before clearing	3	3	3	3	2	1
<u>% cover</u>						
Agrostis gigantea	18	56	7	35	55	47
Anthoxanthum odoratum	44	22	17	43	3	0
Holcus lanatus	0	2	0	0	27	23
Holcus mollis	0	0	0	0	0	0
Carex obnupta	12	19	0	0	2	17
Cirsium arvense	0	2	0	0	10	19
Hypochaeris radicata	1	4	21	18	1	0
Plantago lanceolata	0	3	1	9	5	0
Ranunculus repens	13	5	0	4	11	14
Trifolium repens	0	3	0	8	19	13
Pteridium aquilinum	74	5	41	31	0	0
Rubus laciniatus	0	2	4	0	3	4
Rubus ursinus	5	0	13	2	5	0
Alnus rubra	0	0	0	0	0	1
Frangula purshiana	0	0	7	0	0	0
Picea sitchensis	18	2	61	4	0	0
Tsuga heterophylla	0	0	0	0	0	0

Appendix 3. (continued)

	Site				
	6L-CA	7L-AG	7L-AO	8H-AG	8H-CA
soil % organic matter	3.4	6.8	6.0	9.2	9.4
soil % water	29	40	39	41	37
soil pH	4.6	4.2	4.2	4.1	4.3
soil % sand	72	44	42	67	61
AI - agricultural intensity	3	3	3	3	3
burning before clearing	1	1	1	1	1
<u>% cover</u>					
Agrostis gigantea	36	40	37	64	60
Anthoxanthum odoratum	0	4	23	0	0
Holcus lanatus	22	3	4	31	32
Holcus mollis	0	29	26	0	0
Carex obnupta	0	13	6	0	0
Cirsium arvense	35	6	0	0	48
Hypochaeris radicata	0	0	1	7	0
Plantago lanceolata	1	0	1	12	5
Ranunculus repens	14	10	12	10	25
Trifolium repens	5	7	5	4	0
Pteridium aquilinum	0	0	0	4	0
Rubus laciniatus	3	8	9	0	0
Rubus ursinus	0	0	0	0	0
Alnus rubra	0	0	0	0	0
Frangula purshiana	0	0	1	0	0
Picea sitchensis	0	0	0	0	2
Tsuga heterophylla	0	0	0	0	0

Curriculum Vitae for Dennis A. Riege

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Education

Ph. D.	2000 (Botany) University of Washington, Seattle, USA
M. S.	1976 (Zoology) University of Wisconsin, Madison, USA.
B. A.	1970 (Biology, Chemistry) Manchester College, Indiana, USA

Professional Experience

1996-2000	Ph. D. Dissertation Research and Graduate Teaching Assistant. Botany Department, University of Washington. Research: Arrested old field succession within Pacific Northwest rain forests, particularly on factors that affect Sitka spruce (*Picea sitchensis*) colonization of fields dominated by European pasture species. Courses taught: plant ecology, plant morphology, general biology.
1987-1996 & 2000.	Instructor (summers). University of North Carolina at Wilmington Summer Ventures Program. Coastal ecology courses in program for advanced secondary students. Guided student research projects on ecology of barrier islands and estuaries.
1995	Teaching Associate. Biology Department, University of Washington. Courses taught: general biology.
1992-1994	Instructor. Trident Technical College. Charleston, South Carolina. Human anatomy and physiology, general biology. Excellent student evaluations.
1990-1992	Instructor. Southeastern Community College. Whiteville, North Carolina. Human anatomy and physiology, general biology, zoology.
1989-1992	Instructor (summers or weekends). University of North Carolina at Wilmington Science and Mathematics Education Center. Coastal biology courses for secondary school teachers.
1978-1989	Farm Owner and Operator. Custer, Michigan. Practical agricultural experience was later useful in experimental design of field research.

1978	Biologist. Aquatic Systems, Inc. Ludington, Michigan. Collaborated on study of spawning of Great Lakes fishes.
1971-1976	M. S. Thesis Research and Graduate Teaching Assistant. Zoology Department, University of Wisconsin. Research: Ecology and social organization of coexisting populations of red squirrels (*Tamiasciurus hudsonicus*) and gray squirrels (*Sciurus carolinensis*) in mixed coniferous-deciduous forests. Courses taught: general zoology.

Publications

Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. Journal of Mammalogy 72:152-162.

Organ, W. L., G. L. Towns, M. O. Walter, R. B. Pelletier, and D. A. Riege. 1979. Past and presently known spawning grounds of fishes in the coastal waters of the Great Lakes. Michigan Dept. of Natural Resources Technical Report No. 79-1, 577 p

Riege, D. A. 1976. Red squirrel ecology and coexistence with gray squirrels in northern Wisconsin mixed forests. M. S. Thesis. University of Wisconsin at Madison.

Oral Presentation

August 1999. Ecological Society of America 84th Annual Meeting, Spokane, Washington. Slow succession in old fields within a temperate rain forest: insights from vegetation analysis.

Professional Memberships

Ecological Society of America
International Association of Vegetation Science

Grants and Awards

2000	University of Washington Dissertation Writing Fellowship
1999	University of Washington Chapter of Sigma Xi Grant-in Aid
1997, 1996	University of Washington Botany Department Field Research Endowment
1990, 1989	Grants from Eisenhower Program of North Carolina to fund and teach coastal biology courses for secondary school teachers
1971-1972	University of Wisconsin: Wisconsin Alumni Research Fellowship
1969	Manchester College: Hull Scholarship, for outstanding chemistry students