

Differential Tree Colonization of Old Fields in a Temperate Rain Forest

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ABSTRACT.—Most old fields in the Queets Valley of Olympic National Park, USA, remain dominated by exotic herbs 60 y after abandonment although the fields are surrounded by temperate rain forest. However, areas of some fields have been invaded by *Picea sitchensis*, one of three dominant forest species (with *Alnus rubra* and *Tsuga heterophylla*). This provided an opportunity to examine local variation of factors (competition, facilitation, cervid herbivory, soils) that influence tree colonization within a set of old fields, an approach rare in previous studies. *Picea* sapling invasion of field edges was negatively correlated with percent cover of *Agrostis gigantea* and positively correlated with *Anthoxanthum odoratum*. Potential indicators of competition (sod thickness, thatch thickness, percent ground cover) were correlated with *Agrostis* cover. *Picea* edge invasion was also correlated with soil organic matter. In experiments, seedlings of *Picea* and *Tsuga* emerged as readily in *Agrostis* as in *Anthoxanthum* or *Pteridium aquilinum*, but suffered higher mortality in *Agrostis*. Experimental seedling establishment was low and required reduction of competing vegetation. In experiments with transplanted seedlings, cervid herbivory suppressed growth of *Tsuga* and *Alnus*, but not *Picea*. Growth of *Picea* seedlings was facilitated by *Pteridium*. Differential tree colonization of the fields resulted from: (1) differential competition by invaded cover types against seedling establishment, (2) selective herbivory on tree species of established seedlings and (3) facilitation by fern cover of seedlings of an unbrowsed species.

INTRODUCTION

Abandoned agricultural fields have been used to examine processes of secondary succession. Early studies were in the eastern USA, where typical old fields progressed from pioneer herbs to shrubs and trees in a few decades (Billings, 1938; Keever, 1950; Bard, 1952). This produced a holistic, progressive and deterministic view of old-field succession (Clements, 1916; Odum, 1959). For the last 30 y, an experimental reductionistic approach that examines the mechanisms of succession has dominated studies (Connell and Slatyer, 1977; Pickett *et al.*, 1987; Glenn-Lewin *et al.*, 1992). This approach strongly suggests that old-field succession is an individualistic population process (Gleason, 1926; Pickett, 1982; Keever, 1983), influenced by many biotic and abiotic mechanisms (Pickett *et al.*, 1987). Finegan (1984) reasoned that the relative importance of mechanisms of succession is likely to vary widely between environments. We examined whether the relative importance of mechanisms can differ on a local scale, with individualistic responses to local environmental variation. We studied a set of old fields in the Queets River Valley in Olympic National Park (ONP) to determine how differential tree colonization was related to four factors: competition, facilitation, soils and cervid herbivory. Few previous studies have examined the effects of local differences in plant cover or soils on mechanisms of tree colonization (but *see* Burton and Bazazz, 1991; Berkowitz *et al.*, 1995).

Fields in scattered homesteads in the Queets Valley were abandoned by 1944, after the valley was added to the ONP. Most of the fields have yet to be invaded by trees although they

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are surrounded by temperate rain forest. However, parts of some fields have been colonized by *Picea sitchensis*, providing us with an opportunity to examine factors that control tree colonization. Previous studies of old field succession demonstrated that tree colonization can be inhibited by competition from herbs (De Steven, 1991b; Berkowitz *et al.*, 1995; Prach *et al.*, 1996), cervid herbivory (Myster and McCarthy, 1989; Hill *et al.*, 1995; Lawson *et al.*, 1999) or lack of soil moisture (Myster, 1993). Tree establishment can be facilitated by herbs (DeSteven, 1991a; Gill and Marks, 1991) or by shrubs (Werner and Harbeck, 1982). Comprehensive experimental studies have examined effects of multiple mechanisms on tree colonization (DeSteven, 1991a, b; Gill and Marks, 1991), but these have not emphasized how the relative importance of these mechanisms might vary locally among a set of fields.

Most old-field studies in temperate forest biomes report woody plant invasion within 20 to 30 y (Keever, 1983; Falinska, 1991; Myster, 1993; Smit and Olf, 1998). The few examples of persistent old fields (Inouye *et al.*, 1987; Osbornova *et al.*, 1990; Prach *et al.*, 1996) were associated with infertile xeric conditions that are in marked contrast to the humid climate and fertile soils of the Queets fields. Examination of the Queets fields merits attention in the body of old field studies because it is a case study of a predominantly arrested succession under benign conditions and is a first look at old-field succession in its biome (Pacific Northwest rain forest). Seed dispersal was not a limiting factor because the major species that dominate surrounding forests (*Picea*, *Alnus rubra*, *Tsuga heterophylla*) all produce copious amounts of small wind-blown seeds that disperse readily over distances equal to the size of the fields (Harris, 1967). Although rodent seed and seedling predation is critical elsewhere (Gill and Marks, 1991; Ostfield *et al.*, 1997), predation does not create a major barrier to tree colonization of the Queets fields (Riege, 2000). Harmon and Franklin (1989) found seed predation to be unimportant to regeneration of *Picea* and *Tsuga* in forests of the Pacific Northwest.

In a survey of 11 Queets fields, Riege (2000) discovered that sapling invasion was limited to field edges with specific cover and soil characteristics. We investigated how these cover and soil factors were correlated with the density of *Picea* saplings. Moreover, we conducted experiments to see if and how competition, facilitation or cervid herbivory affected the ability of *Picea*, *Tsuga* and *Alnus* seedlings to colonize the main cover types of the fields.

METHODS

Study areas.—Study plots were in old fields from homesteads scattered along 15 km of the Queets River Valley within ONP, Washington, USA; 47°33–38'N, 124°0–13'W; elevation 50 to 130 m (Riege, 2000). Homesteads were pioneered in the 1890s but were abandoned by 1944. The fields (2.5–8.5 ha) were used for pasture, hay or oats. 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. This is replaced by *Picea sitchensis* and *Tsuga heterophylla* on older terraces (Fonda, 1974). All study fields were on alluvial terraces and were bordered by forests dominated by either *Picea* or *Alnus*. On a soil-age gradient, from low to high terraces, Riege (2000) found increases in soil organic matter (range: 2.3% to 11.2%) and soil moisture (26% to 47%, during a dry June). Soil color changed from dark gray on low terraces to brown on high terraces. Soil texture (range: 35 to 72% sand) was not related to terrace location. Mean annual precipitation is 300 cm, falling mostly as rain between October and May. Mean summer rainfall (June through August) is only 24 cm. Temperatures are mild (monthly means range from 1 to 24 C).

Seven species dominated the vegetation of the former fields. In a sample of vegetation of 11 fields, Riege (2000) found the majority of quadrats dominated by the exotic pasture

grasses *Agrostis gigantea* (45%) and *Anthoxanthum odoratum* (12%). Serial aerial photographs showed that the other five dominants have expanded their cover since field abandonment. These species include two additional nonnatives, the herb *Cirsium arvense* (9%) and shrub *Rubus laciniatus* (8%), and three native species, the sedge *Carex obnupta* (5%), fern *Pteridium aquilinum* (13%) and tree *Picea sitchensis* (8%). Plant nomenclature follows Kartsesz (1994). *Agrostis* occurred in all fields and the other dominants were present in most fields. *Picea* invaded parts (1–3 ha) of three high-terrace fields soon after abandonment. Contemporary *Picea* sapling invasion was virtually limited to cover dominated by *Anthoxanthum* or *Pteridium* on high-terrace soils (brown soils with organic matter $\geq 6.8\%$). Sites within three fields (identified by ONP as Kelly, Streater and Gwin) that varied by cover of the dominants (*Agrostis*, *Anthoxanthum*, *Pteridium*) and soil characteristics were chosen for the experiments on tree colonization described below.

There is a large resident elk (*Cervus elephus roosevelti*) population (Schroer *et al.*, 1993) that browses shrubs and grazes the fields. Deer (*Odocoileus hemionus*) occur, but in much lower numbers. Elk densities are estimated at 6–7 per km² on winter ranges and elk biomass 15 times greater than deer in the western ONP (Woodward *et al.*, 1994). Exclosures in nearby rain forests have shown that browsing shapes understory vegetation by decreasing shrub and fern cover and by increasing grass cover (Schreiner *et al.*, 1996). Elk herbivory also suppresses *Tsuga* regeneration within the forest (Woodward *et al.*, 1994).

Differential Picea sapling invasion.—We conducted a study of sapling invasion of field edges during September–October 1999 to examine relationships among *Picea* colonization, field cover and soil characteristics. Nine plots were chosen subjectively along edges of six different fields to represent different degrees of: (1) *Picea* sapling invasion, (2) cover of *Agrostis*, *Anthoxanthum* and *Pteridium* and (3) soil age. All plots bordered stands of mature *Picea*, which certainly provided an ample seed rain over the decades. Plots were 50 m long and extended 5 m from the edge. All saplings ≥ 25 cm tall (range: 25 to 350 cm; age ranging from ~4 to 14 y) were counted within each plot. Ten 1-m² quadrats were located randomly within each plot to measure plant cover and to sample soils (*Picea* saplings were too few and too young in the plots to have significantly affected plot cover and soil parameters). In each quadrat, percent cover of each plant species was estimated. Sod depth, thatch depth, ground cover and total cover were measured as potential indicators of competition facing *Picea* seedlings. Sod is a layer of soil held together by matted roots. Thatch is an attached layer of interlocking grass stems and leaves above the soil surface. Ground cover was determined as total cover minus that of *Pteridium*, *Rubus laciniatus* and *Vaccinium parvifolium*, each of which forms a canopy above the surface layer. Soil samples were collected in each quadrat. Soil water content was determined gravimetrically (at 105 C) and combusted in a muffle furnace at 450 C for organic matter content (Wilde *et al.*, 1972). Soil texture (sand, silt, clay fractions) was determined by the hydrometer method (Bouyoucos, 1951). Relationships of *Picea* density to cover and soil characteristics were examined by log-linear regression analysis. Relationships of sod, thatch, ground cover and total cover to *Agrostis*, *Anthoxanthum* and *Pteridium* cover were examined by linear regression.

Competition experiments.—Few saplings were present on low-terrace fields. To determine if competition by the sod-forming grass *Agrostis* was a factor that inhibited tree seedling emergence on low-terrace soils, we initiated an experiment in 1998 in Kelly Field. We applied two treatments to decrease both aboveground and rhizome plant mass. At each of five randomly chosen locations, three 1-m² plots were assigned randomly to: (1) untreated control, (2) application of glyphosate (Roundup®), with regrowth periodically clipped and (3) removal of the sod layer and tilling of the remaining soil, with regrowth periodically clipped. Plots were subdivided into four ¼-m² subplots, which were assigned randomly to

Picea, *Tsuga*, *Alnus* and no seeding. Two hundred seeds from local sources were sown per subplot on 23 March 1998. Distributions of numbers of emergent *Picea* and *Tsuga* seedlings were lognormal; hence, logarithmic transformations were applied to counts. Seedling survival was analyzed by randomized block ANOVA followed by Bonferroni comparison of means. Very few *Alnus* seedlings emerged in the field experiments, although they did emerge on field soils in a greenhouse trial (greenhouse emergence on field soils: *Alnus* = 44%, *Picea* = 64%, *Tsuga* = 56%; no difference between low- and high-terrace soils).

Sapling invasion on high terrace fields differed by type of invaded cover. In 1999 a second competition-reduction experiment was designed to determine if tree seedling emergence and early establishment differed among *Agrostis*, *Anthoxanthum* and *Pteridium* cover on high-terrace fields. Five random locations were chosen, within each of these sites: adjacent *Pteridium*, *Agrostis* and *Anthoxanthum* areas in Streater Field and adjacent *Pteridium* and *Agrostis* areas in Gwin Field (*Anthoxanthum* site not available on Gwin). At each location, two 25 × 50-cm plots of similar microtopography and cover were randomly designated as control plots or plots that were partially tilled with a tined hand cultivator then periodically clipped. This treatment retained some original cover yet exposed soil and was meant to reduce competition. Mixtures of 100 seeds each of *Picea*, *Tsuga* and *Alnus* were sown in each plot during early spring (21–22 April) and again in mid-May. Logarithmic transformations were applied to seedling counts. Emergence in early July 1999 was analyzed by a mixed-model randomized block, nested ANOVA, using site as an among-block random effect and tilling as a within-block fixed effect. The number of seedlings present in March 2000 was analyzed by the nonparametric Wilcoxon paired-sample test.

To determine if soil differences affected seedling-emergence results in the 1999 competition experiment, soil samples were taken at all 25 experimental locations. Percent soil organic matter, water, sand, silt and clay were determined by the methods described above. Spearman rank correlations were used to compare the soil properties to number of emergent seedlings in the plots. Soil parameters among the five sites were also compared by ANOVA.

Cervid herbivory experiment.—Observations of field edges indicated that herbivory by elk or deer suppressed growth of *Tsuga* and *Alnus*, but not *Picea*, seedlings. An experiment was designed to quantify this effect using transplanted seedlings and cervid exclosures. We also wished to compare effects of herbivory with that of competition from herbaceous vegetation. Two-y-old bare root seedlings of *Picea* and *Tsuga* were obtained from local nurseries. One-y *Alnus* wild seedlings were excavated from a maintenance yard of ONP. Heights of transplants averaged 38.6 ± 8.0 cm (mean \pm SD) for *Picea*, 38.3 ± 8.2 cm for *Tsuga* and 34.9 ± 10.1 cm for *Alnus*. Maximum widths of the spreading crowns of *Tsuga* transplants averaged 38.6 ± 8.3 cm. Five locations were chosen at Kelly Field to be dispersed among two terraces and *Pteridium* or *Agrostis* cover. *Picea*, *Tsuga* and *Alnus* seedlings were transplanted into blocks of three plots (1.5 × 3 m) at each location during March 1999. Plots were assigned randomly to: (1) no treatment, (2) competing vegetation periodically clipped and removed and (3) enclosed by a woven-wire fence (2.5 m wide × 4 m long × 1.5 m tall to exclude elk and deer) and periodically clipped. We rejected the normal fourth treatment (exclosure without clipping) because exclosures facilitate lush grass growth not comparable to that in control plots. Seedlings were transplanted in an array of three rows and eight columns. Each column contained each species, with pattern shifting regularly in adjacent columns. Survival and height growth were monitored for 1 y. Maximum widths of *Tsuga* crowns were also measured. Relative growth rates (RGR) were used to compare growth of survivors among the treatments. RGR is defined as the change in a growth value over time divided by the value at the start of the period. Survival and RGR of each species were

measured after the growing season in October 1999 and were analyzed by randomized block ANOVA with Bonferroni comparison of means.

Pteridium facilitation experiment.—Preliminary observations suggested that *Pteridium* cover could promote *Picea* invasion. We designed this experiment primarily to investigate facilitation of transplanted *Picea* seedlings by *Pteridium*, but also to compare survival, growth and herbivory of *Picea* seedlings to those of *Tsuga* and *Alnus*. During March 1999 we transplanted seedlings from the same stocks described above at five random locations within four sites: adjacent *Pteridium* and *Agrostis* sites in Gwin Field and adjacent *Pteridium* and *Anthoxanthum* sites in Streater Field. Adjacent sites were on similar soils in each field. Seedlings were transplanted in rectangular arrays (1 × 2.5 m) of 3 rows and 5 columns, in the pattern of the previous experiment. Signs of herbivory were recorded periodically. Seedling growth and survival were measured in October 1999. *Picea* growth rates in *Pteridium* and adjacent grassy sites were compared by *t*-tests. Differential survival among the three species was analyzed by randomized block ANOVA with Bonferroni comparison of means.

RESULTS

Picea sapling invasion of edges.—The number of *Picea* saplings per 250-m² plot ranged from 0 to 106. In linear regression analyses, *Picea* sapling invasion was inversely related to *Agrostis* cover and positively related to *Anthoxanthum* (Table 1). Three indicators of potential competition (sod depth, thatch thickness, ground cover) correlated strongly with *Agrostis* cover, and inversely with *Anthoxanthum* cover (although only the thatch regression was significant). *Picea* sapling density showed significant negative correlations with thatch thickness and ground cover. Density of *Picea* saplings was not related to *Pteridium* cover, which contrasted with an association between *Pteridium* and *Picea* saplings on high terraces found in an earlier study (Riege, 2000). *Picea* sapling density was not related to total cover, which correlated strongly with *Pteridium* cover ($R^2 = 0.61$, $P = 0.01$). Hence the nature of ground cover beneath *Pteridium* fronds was more important than *Pteridium* cover to *Picea* establishment on these plots. Associated with *Agrostis* cover were the rhizomatous forb *Ranunculus repens* and the grass *Holcus lanatus*. The rosette forbs, *Hypochaeris radicata* and *Plantago lanceolata*, were associated with *Anthoxanthum*.

Among the soil properties, *Picea* sapling numbers significantly correlated only with organic matter (Table 1), and not with percent moisture or particle size. *Agrostis* cover and soil organic matter provided the best fits in the simple linear regressions with log number of *Picea* saplings (Table 1). The best multiple regression model (adjusted $R^2 = 0.91$; $P = 0.0006$) incorporated two uncorrelated variables, *Agrostis* cover and silt content: $[\log(Picea \text{ saplings} + 1) = -0.8 + 0.05 * \% \text{ silt} - 0.04 * \% \text{ Agrostis}]$. This suggested that silt content, although showing no independent relationship with *Picea* invasion (Table 1), may be a factor in areas of low *Agrostis* cover (perhaps due to the increased moisture retention of silt).

Effects of competitor reduction on seedling emergence.—In the 1998 experiment removal of *Agrostis* sod on the low-terrace Kelly Field significantly increased *Picea* and *Tsuga* emergence (Fig. 1), although emergence rates were low and variable. Emergence also increased in glyphosate plots, though the effect was not significant. Although glyphosate appeared to kill all aboveground plant material after application, the vegetation resprouted readily. Vegetation also steadily reoccupied the sod-removal plots, but at a slower rate. Thus, the degree of competition in the experimental plots increased over time, despite periodic clipping. *Picea* and *Tsuga* seedlings began to emerge late in May. After a July maximum, their numbers declined during the dry summer. None survived to the following year.

In the experiment on high-terrace fields, competitor reduction did not increase emergence of *Picea* or *Tsuga* by July 1999 (Fig. 2) nor did emergence differ by site. Emergence in

TABLE 1.—Simple linear regression models of *Picea* sapling density against soil and cover characteristics and of the competition indicators against cover of *Agrostis* and *Anthoxanthum*: summary of R^2 and P values. NS = not significant at $P \geq 0.05$ ($n = 9$ edge plots)

	R^2	Sign	P
Log (No. <i>Picea</i> saplings + 1) versus:			
soil			
organic matter (%)	0.76	+	0.002
water (%)	0.02	+	NS
sand (%)	0.01	+	NS
silt (%)	0.02	–	NS
clay (%)	0.03	+	NS
cover			
<i>Agrostis</i> (%)	0.72	–	0.003
<i>Anthoxanthum</i> (%)	0.62	+	0.012
<i>Pteridium</i> (%)	0.12	+	NS
competition indicators			
sod depth (cm)	0.30	–	NS
thatch depth (cm)	0.52	–	0.016
ground cover (%)	0.47	–	0.024
total cover (%)	0.02	–	NS
Sod depth (cm) versus:			
<i>Agrostis</i> cover (%)	0.66	+	0.008
<i>Anthoxanthum</i> cover (%)	0.23	–	NS
Thatch depth (cm) versus:			
<i>Agrostis</i> cover (%)	0.92	+	0.001
<i>Anthoxanthum</i> cover (%)	0.58	–	0.018
Total percent ground cover versus:			
<i>Agrostis</i> cover (%)	0.55	+	0.021
<i>Anthoxanthum</i> cover (%)	0.19	–	NS
Total percent cover versus:			
<i>Agrostis</i> cover (%)	0.23	+	NS
<i>Anthoxanthum</i> cover (%)	0.06	–	NS

Agrostis control plots in the 1999 experiment was higher than in tilled plots in early July (although not significantly). However, seedling numbers decreased more rapidly over the summer in *Agrostis* than in the other cover types. Competitive cover reoccupied the surface of tilled portions of plots over summer, even though aboveground growth was periodically clipped. By March 2000, the competitor reduction treatment did show an effect. Significantly more *Picea* and *Tsuga* seedlings were established in tilled than in control plots (Fig. 2), but they were confined to *Pteridium* and *Anthoxanthum* sites. None remained in *Agrostis* sites. It was notable that seedling-emergence rates of *Tsuga* and *Picea* were similar in the competition experiments, even though *Picea* saplings prevailed in the fields. Differences in seedling emergence and establishment among plots did not correlate with soil organic matter, moisture or particle size. *Agrostis* sites did not differ in soil organic matter from adjacent *Pteridium* or *Anthoxanthum* sites within the same fields. Thus, lack of *Agrostis* cover seemed more important than organic matter to tree seedling establishment in these high-terrace fields.

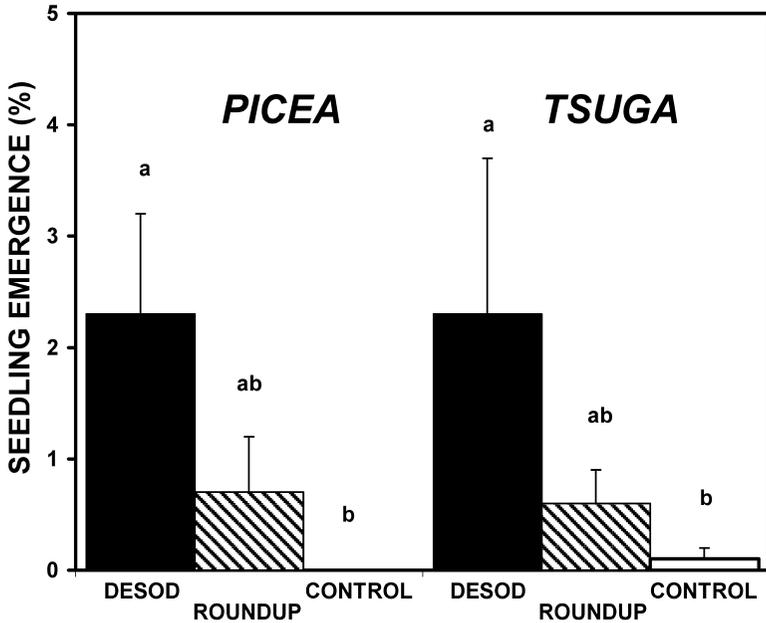


FIG. 1.—Mean (\pm SE) percent seedling emergence of *Picea* and *Tsuga* on 2 July 1998 in *Agrostis* site (Kelly Field). In treatment contrasts of desodded, glyphosate (Roundup) and control, different letters indicate means differ by $P < 0.05$ by Bonferroni comparison after randomized block ANOVA

Effects of cervid herbivory on seedling survival and growth.—Exclusion of elk and deer did not significantly affect survival of the transplanted seedlings of *Picea* (100% in fenced plots, 98% in clipped, 98% in control) or *Alnus* (83% fenced, 85% clipped, 68% control) after one season. However, survival of *Tsuga* decreased outside the enclosures (88% fenced, 65% clipped, 43% control, all differ by Bonferroni comparison at $P < 0.05$). Enclosures did not affect *Picea* growth rates, but growth rates of *Tsuga* and *Alnus* outside the enclosures were reduced significantly (Fig. 3). When released from browsing, relative height growth of *Tsuga* was similar to *Picea*, while *Alnus* was four times that of *Picea*. In addition to the growing-season effect, *Tsuga* was also significantly browsed over winter. All plants surviving in autumn were still alive the following spring, but their RGRs were reduced further (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%). *Tsuga* seedling crowns were trimmed by browsing into a thin cylindrical shape. Competitor reduction by clipping did not increase RGRs of the three species compared to the controls (Fig. 3). However, differences in the amounts of competing herbaceous biomass between clipped and control plots were not large, because elk grazed both types of plots.

Effect of Pteridium on seedling survival and growth.—In both fields, relative growth rates for *Picea* seedlings in October 1999 (Fig. 4) were significantly higher (three times greater) in the two *Pteridium* sites than in the adjacent grass-dominated sites. *Picea* seedling survival (92% overall) did not differ among the four sites. In contrast to *Picea*, browsing suppressed October survival of *Tsuga* to 32% and *Alnus* to 17% ($P < 0.05$, Bonferroni comparison to

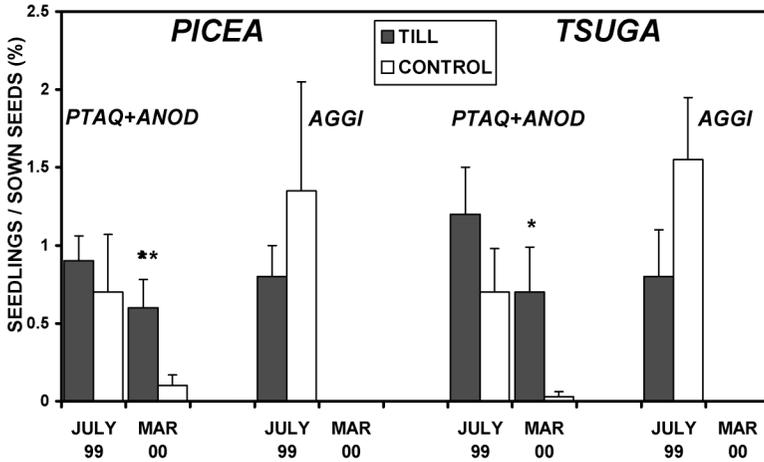


FIG. 2.—Cover-type differences in mean (\pm SE) percent seedling emergence on 8–9 July 1999 and seedling establishment on 20 March 2000 of *Picea* and *Tsuga* in competition experiment (Gwin and Streater Fields). Site values are pooled to show differences between *Agrostis* (AGGI) sites and *Pteridium* (PTAQ) + *Anthoxanthum* (ANOD) sites. Seedling emergence and establishment patterns were similar among *Pteridium* and *Anthoxanthum* sites. Mean emergence in July 1999 among all sites did not differ significantly by ANOVA. Mean establishment in March 2000 of tilled vs. control plots differed by Wilcoxon paired-sample test (* $P < 0.05$; ** $P < 0.01$). No seedlings remained in any *Agrostis* plots in March 2000

Picea after randomized block ANOVA). Survival or growth of *Tsuga* or *Alnus* was not facilitated by *Pteridium*; cervid herbivory was the critical factor affecting these species.

DISCUSSION

Competition.—The dominant species of the surrounding forests—*Picea sitchensis*, *Alnus rubra* and *Tsuga heterophylla*—seldom became established on abandoned Queets fields, although *Picea* could invade some sites on higher terrace fields that were dominated either by *Anthoxanthum odoratum* or *Pteridium aquilinum*. Our study indicated that the first barrier to tree colonization was competition from herbaceous field vegetation. Natural *Picea* invasion of field edges was negatively correlated with abundance of *Agrostis gigantea*. Characteristics that suggest increased competition (sod, thatch, ground cover) were positively correlated with *Agrostis* cover, and sod removal permitted *Picea* and *Tsuga* to emerge in a low-terrace *Agrostis* site. Experiments with sown seeds demonstrated that seedlings of *Picea* or *Tsuga* emerged as readily in *Agrostis* as in *Pteridium* or *Anthoxanthum* in high-terrace fields, but that they then suffered higher mortality. Competition from the sod-forming *Agrostis* and its rhizomatous associates appears to have caused seedling death. Natural *Picea* invasion in our fields was positively correlated with dominance by the bunchgrass *Anthoxanthum*, which forms neither sod nor thatch. Even in cover dominated by *Anthoxanthum* or *Pteridium*, establishment from seed in our experiments required a treatment that decreased competition.

Turf-forming grasses with a dense sod of matted roots and thick ground cover make a formidable barrier to establishment by small-seeded species. Prach *et al.* (1996) reported that turf removal was necessary for seedling establishment of *Picea abies* in experiments in a 50-y-old sod grass field in the Czech Republic. Coates *et al.* (1993) found that sods reduced

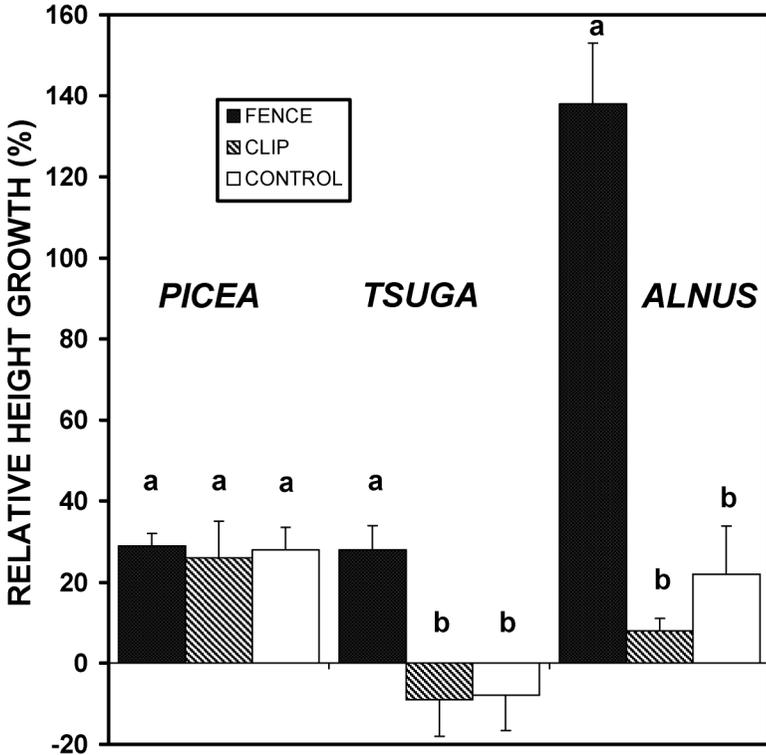


FIG. 3.—Mean (\pm SE) percent relative growth rates (RGRs) in height of transplanted seedlings of *Picea*, *Tsuga* and *Alnus* in cervid exclosure experiment. Seedlings were planted 21–26 March 1999 and measured 24 October 1999. Seedlings were transplanted: within fenced exclosures with herbaceous growth clipped (FENCE); outside exclosures with herbs clipped (CLIP); and outside exclosures with no clipping (CONTROL). Within each species, different letters indicate means differ by $P < 0.05$ by Bonferroni comparison after randomized block ANOVA

growth rates of *Picea sitchensis* seedlings more than did bunchgrass. In local forests, Harmon and Franklin (1989) concluded that *Picea* and *Tsuga* regeneration is confined almost exclusively to nurse logs because competition from ground cover excludes them from the forest floor. Thus, we are not surprised that these small-seeded species have difficulty establishing in dense cover in the old fields. Furthermore, most *Picea* and *Tsuga* seedlings did not emerge until July, during the dry season. *Picea* and *Tsuga* seedlings grow slowly and are susceptible to moisture stress (Gray and Spies, 1997).

Soils.—Natural *Picea* and *Tsuga* establishment was almost completely restricted to high-terrace Queets fields. Soil properties that increased with terrace age were organic matter and percent moisture. Organic matter was more important than percent moisture to *Picea* sapling establishment in our edge study. The increase of *Picea* invasion with soil organic matter may be due to organic content directly, to moisture retention or to coincidence. Since most *Picea* regeneration in Pacific Northwest forests occurs on decaying nurse logs, organic material may promote germination and early growth. The contribution made by soil organic matter to moisture retention (Hudson, 1994) may also benefit *Picea* survival during summer droughts. Another possibility is that soil organic matter does not enhance *Picea*

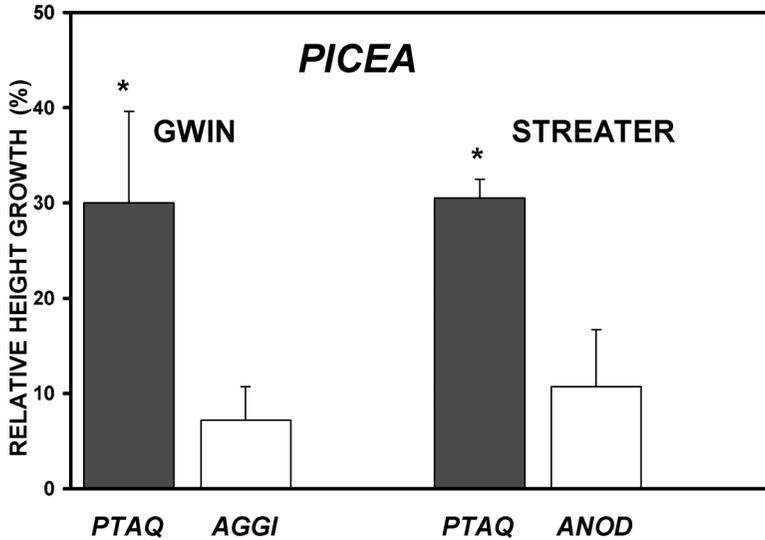


FIG. 4.—Mean (+SE) percent relative growth rates (RGRs) in height of transplanted seedlings of *Picea* among sites in facilitation experiment (Gwin and Streater Fields). Seedlings were planted 23–24 March 1999 and measured 23–24 October 1999. An asterisk (*) indicates significant difference ($P < 0.05$ by t -test) between mean RGR of *Pteridium* (PTAQ) site (shaded) and adjacent grass-dominated (AGGI = *Agrostis*, ANOD = *Anthoxanthum*) sites (unshaded)

colonization but coincidentally covaries with an unidentified causal factor that increases with soil age.

Cover type was more important than soil type to *Picea* invasion of the Queets fields. When the sod grass *Agrostis* was dominant on high-terrace soils with high organic matter, little invasion occurred. Burton and Bazazz (1991) also found that tree seedling emergence was influenced more by cover than soil type among eight communities on three soils in Illinois old fields. While plant cover directly affects tree establishment through competition, soils may indirectly affect tree establishment by determining the competing herb species. Soil fertility differences that we did not measure may have affected tree colonization indirectly by influencing species composition. *Agrostis gigantean*, *Ranunculus repens* and *Holcus lanatus* often occur on fertile soil, while *Anthoxanthum odoratum*, *Hypochaeris radicata* and *Plantago lanceolata* indicate infertile soils (Thurston, 1969; Grime *et al.*, 1988; Klinka *et al.*, 1989). Olf and Bakker (1991) found that cover of *Holcus lanatus* and *Agrostis stolonifera* declined with decreasing fertility in Dutch hay fields, while *Anthoxanthum odoratum* and *Plantago lanceolata* increased. Smit and Olf (1998) found that woody species colonized old fields more rapidly on infertile soils, but were excluded from dense swards growing on fertile loams.

Cervid herbivory.—Herbivory by elk and deer did not affect *Picea*, but strongly limited the success of *Tsuga* and *Alnus* seedlings that managed to overcome the barriers to seedling emergence. *Tsuga* seedlings emerged from seed as readily as *Picea* in our competition experiments, and *Tsuga* seedlings grew as fast as *Picea* in our enclosure experiments. However, outside the elk fences, *Tsuga* suffered substantial decreases in survival, height and crown width during the growing season, and a further decrease in size over winter. Thus, freedom from herbivory was the main factor in *Picea* being a much more successful colonizer

than *Tsuga*. Cervid herbivory (by white-tailed deer, *Odocoileus virginiana*) has been found to influence the relative abundance of different tree species that colonize eastern U.S. old fields (Inouye *et al.*, 1994; Hill *et al.*, 1995), although these studies do not report near exclusion of a species, as is the case with *Tsuga* in our fields.

The species composition of the Queets fields indicated that the vegetation has been influenced by elk. Northern European pasture grasses and forbs dominated these meadows. The five major invading species (*Carex obnupta*, *Cirsium arvense*, *Pteridium aquilinum*, *Rubus laciniatus* and *Picea sitchensis*) are either 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 redwood forests of Northwestern California (Harper, 1962). In European lowlands grazed by large mammals, Olff *et al.* (1999) described a vegetation mosaic similar to the Queets fields—patches of unpalatable species in a matrix of pasture herbs. Elk grazing may indirectly slow succession on the Queets fields by maintaining competitive cover, such as *Agrostis*, that in turn inhibits tree establishment. Grazing is known to inhibit succession when seral species, such as grasses, are adapted to defend against herbivores with rapid compensatory growth in favorable environments (Davidson, 1993).

Facilitation.—DeSteven (1991a) and Gill and Marks (1991) found occasions of herb facilitation of tree seedling emergence in old fields during drought. We found no evidence of facilitation of seedling emergence during the dry summer in our experiments (facilitation would be indicated if reduction of a cover species in the competition experiments significantly decreased tree seedling emergence). However, once *Picea* seedlings were established, we found facilitation of growth by *Pteridium* cover. *Picea* seedlings may fare better in *Pteridium* because shading reduces moisture stress during the dry summers at ONP. Berkowitz *et al.* (1995) reported increased survival of tree seedlings beneath herb and shrub cover during a drought year. Although *Pteridium* appeared to facilitate growth of *Picea* seedlings once they become established, the edge study suggested that *Anthoxanthum* cover was more important than *Pteridium* to *Picea* colonization. Overall, in the Queets fields, facilitation has been less important than competition as a mechanism controlling tree colonization, as evidenced by the lack of tree seedling establishment in most field areas. Bellingham *et al.* (2001) found that differential effects of facilitation by a nitrogen-fixing shrub was the probable cause of differential tree colonization of three species in a New Zealand primary succession. However, on our fields, differential facilitation did not cause *Picea* to prevail; cervid herbivory was so detrimental to *Tsuga* or *Alnus* that it precluded any significant facilitative effects of *Pteridium* on those two species.

Conclusions.—Current models of plant succession emphasize individualistic population characteristics and interactions with the abiotic and biotic environment (Noble and Slatyer, 1980; Walker *et al.*, 1986; Walker and del Moral, 2003). This approach can explain why succession in most Queets fields is arrested. The small seeds of *Picea*, *Tsuga* and *Alnus* are ill adapted to establish in dense cover. These tree species face an environment that is likely novel to their evolutionary history in the thick turf produced by exotic rhizomatous species like *Agrostis gigantea*. Most *Picea* and *Tsuga* seedlings do not emerge until late spring, grow slowly, are susceptible to summer drought and compete poorly with herbs (Harmon and Franklin, 1989; Gray and Spies, 1997). *Alnus* germinates best on exposed mineral soil (Schopmeyer, 1974). In contrast, tree invaders of eastern USA fields are typically *Pinus* spp., with seeds 5 to 10 times larger than those found here or larger-seeded species such as *Quercus*.

Our data indicate that competition is a primary barrier that prevents tree colonization of the Queets fields. Natural or experimental reduction of competition enhances colonization (though mature soils may also help). Elk herbivory is a secondary filter that inhibits *Tsuga*

and *Alnus*, but not *Picea*. Elk grazing may also indirectly slow succession by maintaining the competitive herb cover. Growth of the unbrowsed *Picea* seedlings that are able to establish in less-competitive cover may be facilitated by *Pteridium*. Our study demonstrated that the relative importance of competition, facilitation and soils on tree colonization can vary locally within and among a set of old fields. The effects of cervid herbivory also varied among species. These results argue for a multifactorial approach in comprehensive studies of mechanisms of old field succession, in which researchers replicate experiments across the range of local conditions.

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