Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests[1]

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Abstract: Successful regeneration of some species may be linked to microsite availability, which in turn may be influenced by dominant canopy species. We investigated the relationship between canopy feedbacks and microsite heterogeneity as they affect conifer regeneration in two Minnesotan mixed species forests: *Abies balsamea* (L.) Miller-*Populus tremuloides* Michx and *Thuja occidentalis* L.-*Betula papyrifera* Marshall. Objectives were to examine (*i*) microtopographic differences resulting from canopy feedbacks and (*ii*) conifer regeneration at three stages (seed dispersal, germination and establishment). We quantified seed rain and surveyed microtopography and regeneration of *T. occidentalis* and *A. balsamea*. Microtopographic features included pits, mounds, stumps, logs, and level ground. Differences in microtopography beneath deciduous and conifer canopy types were generally minor. Conifer seeds fell in larger numbers under conifer canopy types than under adjacent hardwood canopy types in both forest types, but substantial seed rain occurred up to 20 m into hardwood canopy patches. In the *Thuja-Betula* stands, both germinants and seedlings of *T. occidentalis* occurred almost entirely under the *Thuja* canopy type, and there predominantly on decayed wood (rotting stumps and logs), which occupied only a small fraction of the forest floor. In the *Abies-Populus* stands, *A. balsamea* germinants and seedlings were relatively common beneath both canopy types and on all microtopographic features. The distribution of *T. occidentalis* was more restricted than that of *A. balsamea*, indicating that *A. balsamea* may be more of a generalist.
Keywords: feedbacks, microsite heterogeneity, microtopography, microfeature, canopy type, conifer regeneration, mixed-species forests.

Résumé: La régénération de certaines espèces végétales semble être dépendante de la disponibilité de microsites, disponibilité pouvant être influencée par les espèces dominant la canopée. Nous avons étudié la relation entre la dynamique du couvert forestier et l'hétérogénéité des microsites, et son effet sur la régénération d'espèces de conifères dans deux forêts mixtes du Minnesota, l'une dominée par *Abies balsamea* et *Populus tremuloides*, et l'autre par *Thuja occidentalis* et *Betula papyrifera*. Notre objectif était d'étudier les différences microtopographiques résultant de la dynamique du couvert forestier et les diverses étapes menant à la régénération d'espèces de conifères (dissémination et germination des graines et établissement des plantules). Nous avons donc estimé la pluie de graines, décrit la microtopographie et suivi la régénération de *T. occidentalis* et *A. balsamea*. Les formes microtopographiques comprenaient les dépressions, les monticules, les souches, les bûches et le sol plat. Les différences de microtopographie sous des canopées de type décidu ou de type conifèrien étaient généralement mineures. La pluie de graines des conifères était plus abondante sous un couvert conifèrien que sous un couvert décidu dans les deux types de forêts; cependant, une quantité substantielle de graines de conifères était disséminée jusqu'à 20 m à l'intérieur de plaques de couvert décidu. Dans les peuplements de *Thuja* et *Betula*, la germination des graines et l'établissement des plantules de *T. occidentalis* étaient pratiquement limitées au couvert de *Thuja* et se produisaient surtout sur des substrats de bois en décomposition (souches et bûches), lesquels occupaient seulement une petite portion du parterre forestier. Dans les peuplements d'*Abies* et de *Populus*, la germination des graines et l'établissement des plantules d'*Abies* étaient communs sous les deux types de couvert et sur toutes les formes microtopographiques. La répartition de *T. occidentalis* était donc plus restreinte que celle d'*A. balsamea*, suggérant que *A. balsamea* est une espèce plus généraliste.
Mots-clés: forêts mixtes, hétérogénéité de microsites, microrelief, microtopographie, régénération de conifères, rétro-actions, type de couvert.

Introduction

Dominant species may alter the local microenvironment sufficiently to positively or negatively influence the likelihood of their own and other species' successful regeneration and thus the future stand composition (Woods, 1979; 1984; Roberts, 1992; Wilson & Agnew, 1992; Oliver & Larson, 1996). In forests, common microsites include decaying wood (Scott & Murphy, 1987), and pits and mounds resulting from windthrown trees (Hutnik, 1952; Beatty, 1984), all of which may be affected by the composition and identity of dominant overstory species. Differential survival of tree

seedlings in microsites can influence the composition and spatial heterogeneity of forests (Harmon & Franklin, 1989). Such feedbacks may be important in determining vegetation dynamics and heterogeneity in forest ecosystems (Frelich *et al.*, 1993; Frelich & Reich, 1995a)

Forest floor microtopography varies among forests and between patch types within a given forest (Falinski, 1978; Maser & Trappe, 1984; Huenneke & Sharitz, 1986; Webb, 1988). We use the term "microtopography" as defined by Huenneke & Sharitz (1986): "the patterning of substrates and objects on the scale of an individual plant or seed." Forest floor microtopography often reflects site disturbance

history. Some disturbances, such as clear-cutting and fires, take place on large spatial scales. Other disturbances, such as individual treefalls, operate at smaller scales. In many forest ecosystems, individual canopy tree deaths are the most common natural disturbances leading to fine scale heterogeneity. Mature tree mortality occurs in a variety of ways, each affecting microtopography differently (Putz *et al.*, 1983). Stumps are created when either a live or standing dead tree snaps, rather than uproots. Stumps may also result from logging or thinning operations. Decaying logs result from the fall of either a dead or live tree. Uprooting of living trees result in pits created by displaced soil and adjacent mounds of soil, containing the root system (Beatty & Stone, 1986).

Small-scale disturbances can collectively alter community dynamics (*e.g.*, regeneration patterns) by changing forest floor microtopography (McCarthy & Facelli, 1990). From seed dispersal to seedling establishment and survival, a complex set of factors determines recruitment patterns (Holcombe, 1976; Macguire & Forman, 1983; Huenneke & Sharitz, 1986; Johnson & Fryer, 1992; Houle, 1995). Many microtopographi features (microfeatures) may serve as "safe sites" (*sensu* Harper *et al.*, 1961) for the germination and establishment of seedlings (Curtis, 1946; Nelson, 1951; Clements, 1963; Beatty & Stone, 1986; Scott & Murphy, 1987; Webb, 1988; Alverson, Kuhlman & Waller, 1994; St. Hilaire & Leopold, 1995). Late-successional conifers may require specific safe sites, such as decayed wood, for germination and establishment (Holcombe, 1976; Harmon & Franklin, 1989). In the Great Lakes Region of the United states (including Minnesota, Wisconsin, and Michigan), reduced recruitment of late-successional conifers, such as hemlock (*Tsuga canadensis* [L.] Carriére), balsam fir (*Abies balsamea* [L.] Miller), and white cedar (*Thuja occidentalis* L.), might be linked to reduced safe sites for regeneration (Mladenoff & Stearns, 1993).

A number of studies have examined the link between canopy feedback and forest floor heterogeneity (Beatty, 1984; Woods, 1984; Webb, 1988; Harmon & Franklin, 1989; Collins, 1990). Others have investigated seed dispersal patterns as an aspect of canopy feedbacks that can affect seedling distribution (Bartlett, Reader & Larson, 1991; Ferrari, 1993; Houle, 1995). We have integrated aspects of both approaches by examining seed input at the same sites where feedbacks and microtopographic heterogeneity are explored.

Our investigation of canopy feedbacks and microtopographic heterogeneity concentrated on conifer regeneration at three different stages: seed dispersal, germination, and establishment. We studied two paired stands of two mixed deciduous-conifer forest types: *Thuja occidentalis-Betula papyrifera* Marshall and *Abies balsamea-Populus tremuloides* Michx. We chose these study sites (see study sites, below) because each contained distinct patches with canopies dominated by either a deciduous or a conifer species. The use of two, mixed species forest types with patchy overstory patterns allowed a comparison of the regeneration requirements of two late-successional conifers, *Abies balsamea* and *Thuja occidentalis*. The number of stands in which *Abies balsamea* dominates are becoming increasingly rare in

the state of Minnesota, and *Abies balsamea* has a higher than average mortality rate in comparison with other species (Miles, Chen & Leatherberry, 1990). Although the number of stands in which *Thuja occidentalis* dominates is on the increase in Minnesota (Miles, Chen & Leatherberry, 1990), upland white cedar forests are rare in comparison with the conifer swamps in which they occur (L. Frelich, pers. comm.). (Hereafter, forest and canopy types will be referred to by genus only, and seedlings will be referred to by an abbreviated genus followed by species. Plant nomenclature follows Gleason & Cronquist [1991]).

Within the general context of the ways in which overstory feedback and forest floor heterogeneity affect future forest composition, we addressed the following questions: (*i*) How does conifer regeneration correspond to seed dispersal patterns? (*ii*) Does microtopography differ beneath two canopy types in the same forest? (*iii*) Is seedling distribution correlated with certain microfeatures or canopy types? (*iv*) Do environmental variables differ among microfeatures and between patch types?

Material and methods

STUDY AREAS

THUJA OCCIDENTALIS-BETULA PAPYRIFERA FOREST

We studied two cold-temperate *Thuja-Betula* stands, 3 km apart, within Split Rock Lighthouse State Park (47° N, 91° w) on the north shore of Lake Superior in northeastern Minnesota. In the late 1800s and early 1900s, most of the original north shore forests were logged (Fritzen, 1968, unpubl.). Average annual temperature is 4.7°C and mean total annual precipitation is 739 mm (Midwestern Climate Center, Illinois State Water Survey, Champaign, Illinois). Using the classification scheme from Frelich & Reich (1995a), we characterized the *Thuja-Betula* stands as a *Betula* matrix with a *Thuja* inclusion, *Betula*-dominated patches occupying > 50% of the study area. Basal area in *Thuja*-dominated patches was 53.0 ± 7.8 m²/ha (mean ± SE) and in *Betula*-dominated patches was 34.7 ± 4.0 m²/ha. Stems in conifer patches were around 42% *Thuja*, 21% *Populus balsamifera* L., and 16% *Abies*. Deciduous patches contained 53% *Betula*, 33% *Populus balsamifera* and 2% *Thuja* stems.

Stand 1 (TB1) is a 0.6-ha area, with gently sloping topography and a southwesterly aspect. Soils are of the Hibbing series (Minnesota Department of Natural Resources, 1980, unpubl.) and are well-drained to moderately well-drained. The A horizon consists primarily of a silt loam, but includes both silty clay loam and sandy clay loam. Mean age, an average of counts of 12 cores taken at breast height, for *Betula* was 55.4 ± 3.6 years and for *Thuja* was 94.6 ± 5.4 years. Stand 2 (TB2) is a relatively level 1.2-ha area. Soils are Quetico-Rock (Minnesota Department of Natural Resources, 1980, unpubl.) and are poorly-drained. The A horizon consisting largely of silt-loam and inclusions of silty clay loam and sandy clay loam. Mean age at breast height for *Betula* was 60.4 ± 1.6 years and for *Thuja* was 91.6 ± 1.7 years. Although both stands are upland, TB2 is wetter, with the water table closer to the soil surface.

ABIES BALSAMEA-POPULUS TREMULOIDES FOREST

We studied two cold-temperate *Abies-Populus* stands (11 km apart) on Carlton County land within the Nemadji River watershed, east-central Minnesota. Prior to clear-cutting in the late 1800s, the dominant canopy species of the watershed was eastern white pine (*Pinus strobus* L.) (M. Rasmussen, pers. comm.). Average annual temperature is 4.2°C and mean total annual precipitation is 777 mm (Midwestern Climate Center, Illinois State Water Survey, Champaign, Illinois). Using the classification scheme from Frelich & Reich (1995a), the *Abies-Populus* stands were characterized as a mixture of the two species, with > 90% of the study area consisting of patches < 0.25 ha. Basal area in *Abies* patches was 25.2 ± 3.0 m²/ha (mean ± SE) and in *Populus* patches was 17.5 ± 2.5 m²/ha. *Abies* constituted around 54% of stems in conifer patches, followed by 27% *Populus* and 7% *Picea glauca* (Moench) Voss. Stems in deciduous patches were 46% *Populus*, 15% *Abies*, and 12% *Fraxinus nigra* Marsh.

Stand 1 (AP1) is a 0.7 ha area (46° 28' N, 92°35' W) with nearly-level to hilly topography. Surface soils are of the Ontonagon series and are well-drained to moderately well-drained (Lewis, 1978). The A horizon ranges from silty clay to sandy loam with inclusions of clay and sand. Mean age at breast height for *Populus* was 43.2 ± 3.6 years and for *Abies* was 44.1 ± 3.4 years. Stand 2 (AP2) has a total of 0.9 ha (46° 27' N, 92° 33' W), divided into two sections measuring 0.8 ha and 0.1 ha to avoid a 0.4 ha area in which ice storms, spruce budworm [*Choristoneura fumiferana* (Clem) (Blais, 1985)], and consequent windthrow recently damaged the stand. Topography is nearly level. Soils are of the Nemadji series (Lewis, 1978). The A horizon ranges from sand to loamy sand with inclusions of silt loam. Mean age at breast height for *Populus* was 51.0 ± 2.6 years and for *Abies* was 40.9 ± 2.4 years.

SEED DISPERSAL

To determine whether wind-dispersed conifer seeds were distributed differently beneath deciduous and conifer-dominated canopy types in mixed species stands, transects running from conifer patches into deciduous patches were established at one stand per study area. Transects extended from the interior of conifer patches into deciduous patches. In the *Thuja-Betula* stand (TB2), transects were oriented at six different compass azimuths (*i.e.*, 45°, 105°, 165°, 225°, 285°, and 345°) because wind direction is unpredictable near Lake Superior during the fall, when *T. occidentalis* seed dispersal occurs. Ten circular seed traps (area = 126 cm²) were spaced at 10 m intervals along each transect, for a total of 60 traps. Three traps on each transect were under *Thuja* canopy, one at the border between patch types, and six under *Betula* canopy. Traps were constructed of a wire hoop with three pairs of legs. The corner of a cattle feed sack was suspended from each hoop (Ferarri, 1993).

In the *Abies-Populus* stand (AP1), transects were only oriented at two azimuths running parallel and perpendicular to the prevailing wind direction (45° and 315°, respectively). Nine transects were established, five at 45° and four at 315°. Seven traps per transect were placed 5 m apart, three under the *Abies* canopy, one at the *Abies-Populus* border,

and four under the *Populus* canopy. Traps were square, and ranged in size from 625 cm² to 10 000 cm². Larger traps were placed farthest from the conifer patches. Wire mesh tops excluded much of the leaf litter and seed predators from the sample. Seed trap contents were collected at both sites in late October 1994. Samples were oven dried at 65°C for three days. Seeds of the predominant conifer species at each site were separated from leaf litter and counted. Data from both stands were converted to numbers of seeds/m².

SURVEY OF MICROTOPOGRAPHY

We adapted Webb's (1988) methods to quantify aerial coverage of five kinds of microfeatures at each site: pits, mounds, stumps, logs, and level ground. All microfeatures large enough to be distinguished visually falling within strip plots (width = 2 m) were included in the survey. Strip plots were located systematically, spaced at 20-m intervals in the *Thuja-Betula* stands and at AP2, and at 10-m intervals at AP1. Spacing was adjusted in order to obtain a representative sample in light of differences in stand shape, size, and pattern. In the *Thuja-Betula* stands, strip plots contained 12% of the stand area at TB1 and 6% of the stand area at TB2. In the *Abies-Populus* stands, we sampled 11% of stand area at AP1 and 8% of the stand area at AP2. We also recorded canopy type for each length of strip plot. If over 50% of stems of canopy trees were coniferous, canopy type was labeled conifer. Otherwise, canopy type was labeled deciduous.

Several characteristics of each microfeature were recorded, including approximate shape and dimensions from which aerial coverage was calculated. Aerial coverage was defined as the projected area occupied by a microfeature rather than the surface area. Mounds, pits, and stumps were treated as circles (area calculated as πr^2) or ellipses (area calculated as $\pi[(a + b)/4]^2$) and logs were treated as trapezoids (area calculated as $1/2[a + b]h$) (Scott, 1984). The remaining strip plot area not occupied by any of the above features was defined as level ground.

The age of each microfeature was estimated on the basis of associated decaying wood using the criteria of Franklin *et al.* (1981) adapted for Minnesota by Webb (1988). Webb's (1988) age classes were substituted with numerical ordinal classes for the purposes of this study.

(0) Recent: bark intact, small twigs present, wood firm.

(1) Moderately old: bark only partially intact, small twigs absent, wood firm, logs still off ground.

(2) Old: bark mostly separated from sapwood and sloughed off (except in paper birch), large branches present, wood soft, logs mostly on ground.

(3) Very old: bark absent or only fragments remaining (except in paper birch: only bark remains), wood very soft and usually covered with vegetation, logs on ground.

(4) Extremely old: no wood remains; applies to mounds and pits that no longer have associated wood. This age class may also include glacial features or features resulting from processes other than tree falls.

SURVEY OF NATURAL REGENERATION

At each of the four stands, we established a network of 50 circular plots during the summer of 1994. Half the plots

were placed under each canopy type (25 under conifer and 25 under deciduous), and of these, five were on each of the following microfeatures: pits, mounds, stumps, logs and level ground (Figure 1). Plots were randomly selected from a pool of microfeatures that met a minimum area (0.78 m²) requirement. Logs and stumps surveyed fell within decay class 3 or 4, as did the decaying wood associated with mounds and pits. Our stratified random design was similar to Beatty's (1984).
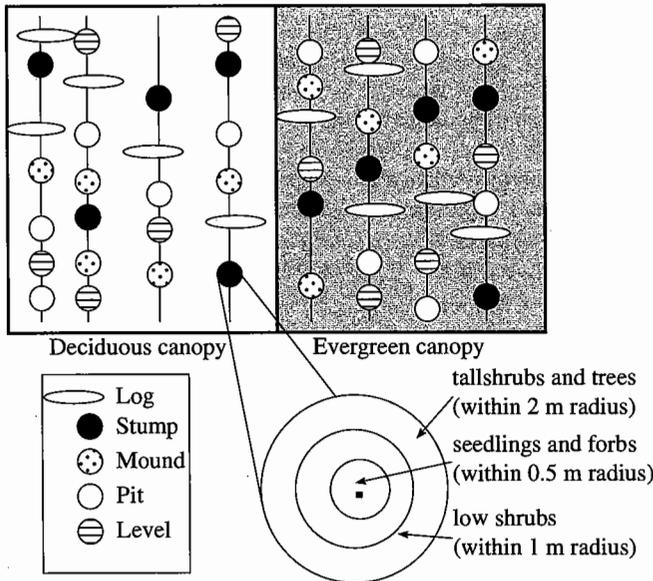

FIGURE 1. Schematic diagram for survey layout (not to scale). 25 survey points were located under each of 2 canopy types (25 points × 2 canopy types × 2 stands × 2 forest types) = 200 survey points. Seedlings and forbs were tallied within 0.5 m from the center. Low and tall shrubs were censused within 1 m and 2 m of the center, respectively. Trees were also censused within 2 m of the center.

We censused all tree seedlings, shrubs, and herbaceous plants at each plot during the spring of 1994. We counted *T. occidentalis* and *A. balsamea* germinants (emerged from seed in 1994) and seedlings (> 1 year old) within a 0.5 m radius of the plot center. Low shrubs (< 1.5 m tall) were counted within 1 m of the center and tall shrubs (>1.5 m) and trees (> 4.0 cm d.b.h.) within 1 m and 2 m of the center, respectively.

We determined gravimetric soil moisture by brushing aside leaf litter and extracting a shallow core (depth = 4 cm, diameter = 3 cm) from the center of each plot at the time of peak germination (early June). Samples were weighed, oven dried (70°C for 72 hours), and weighed again. Moisture content was expressed as percent dry mass. Soil temperatures were measured in June 1995 (thrice per plot) using a thermometer with a 15.5 cm stainless steel stem with a bimetal sensor in the lower 5.2 cm. For each plot, we also measured thickness of leaf litter (three replicates near the plot center) at the time of germination. Exceptions to this were stumps and logs for which no measurable litter occurred except in crevices. For analytical purposes, litter depths for these features were treated as 0.01 cm. Light availability was estimated using canopy openness measure-

ments taken with paired LAI-2000 (Licor Inc., Lincoln, Nebraska) plant canopy analyzers under full-leaf conditions, 10 cm above the center of each plot (September 1994).

DATA ANALYSES

Seed dispersal data were analyzed with a regression model of square-root transformed count data against distance from conifer patch edge. Differences between microfeature aerial coverage under different canopy types at each site and under like canopy types across sites (*e.g.*, comparison of microfeatures under the *Thuja* and *Abies* canopy types) were evaluated with two tailed *t*-tests. Each strip plot was treated as an individual replicate. Differences among measured characteristics (*e.g.*, litter depth and percent soil moisture) among microfeatures and beneath different canopy types were evaluated with two way ANOVAs. Power transformations were used when appropriate, usually to normalize distributions. Differences between microfeatures were then determined with a Tukey-Kramer honestly significant difference test (HSD) (Sokal & Rohlf, 1995), because this test can be set for an exact alpha level if sample sizes are the same and is conservative if sample sizes are different (JMP 3.0, SAS Institute, Cary, North Carolina).

Seedling associations with particular microfeatures, canopy types, and other measured variables were determined using a Poisson regression with an over-dispersion parameter followed by an analysis of deviance (McCullagh & Nelder, 1983; Statistix, Analytical Software, St. Paul, Minnesota). Poisson regression is classified as a generalized linear model. We used Poisson regression because the response variable was a count of numbers of germinants or established seedlings under different conditions. The distribution was asymmetrical, and was initially assumed to follow a Poisson distribution (Lindenmayer *et al.*, 1991). Full model runs included the following categorical and continuous variables: microfeature, canopy type, litter depth, soil moisture, soil temperature, canopy openness, percent herbaceous cover, percent low shrub cover, and percent tall shrub cover. These variables were used as predictors of seedling densities for both *A. balsamea* and *T. occidentalis*. Since many observations were dropped from the full model because they were missing one or more of the measured variables, a partial model using only the two categorical variables was also run so that all observations could be included. Poisson regression results (14 tables) for both full and categorical models are available from the authors. Results from categorical models were followed by a Wilcoxon two sample test (Sokal & Rohlf, 1995; JMP 3.0, SAS Institute, Cary, North Carolina) using a chi-squared statistic with one degree of freedom.

Results

SEED DISPERSAL

Differences in 1994 conifer seed dispersal patterns under different canopy types occurred in both the *Abies-Populus* and the *Thuja-Betula* stands. The ratio of conifer seeds falling under the conifer canopy type: the deciduous canopy type in the *Thuja-Betula* stand was ≈ 7.3:1 and in the *Abies-Populus* stand was ≈ 1.4:1. In the *Thuja-Betula*

stands, numbers of *T. occidentalis* seeds falling within the *Betula* patch decreased with distance from the interior of the *Thuja* patch ($r^2 = 0.87$; $p < 0.0001$) (Figure 2a). *A. balsamea* seed rain and distance from the conifer patch interior were slightly negatively correlated, but the trend was not significant ($r^2 = 0.28$; $p = 0.29$), (Figure 2b). Comparing across sites, *T. occidentalis* seed rain under the *Thuja* canopy was nearly 17 times greater than for the larger-seeded *A. balsamea* under the *Abies* canopy. In 1995, numbers of *T. occidentalis* germinants occurring in *Thuja-Betula* stands were ten times higher than in 1994 (Figures 3a, b), possibly indicating a larger seed rain in 1994 than in 1993.

SURVEY OF MICROTOPOGRAPHY

Dramatic differences in percent aerial coverage, density, size, and decay class of microfeatures occurred between sites. Overall, microsite heterogeneity was greater in *Thuja-Betula* stands than in the *Abies-Populus* stands (Tables I and II). Differences in percent aerial coverage, density, size and decay class between conifer and deciduous patches within each forest type were generally minor (Table I). Logs in decay class 3 occupied a larger percentage of the forest floor under the *Thuja* canopy type than the under the *Betula* canopy type ($t_{[17]} = 1.84$; $p = 0.08$) (Table II).

ENVIRONMENTAL CONDITIONS

Environmental conditions followed similar trends in both forest types. Percent soil moisture, substrate temperature, and litter depth differed between microfeatures in both the *Thuja-Betula* stands, ($p = 0.007$, $p < 0.0001$, and $p < 0.0001$, respectively) and the *Abies-Populus* stands ($p < 0.0001$, $p < 0.0001$, and $p = 0.03$, respectively), (Table III). Substrate temperatures for pooled microfeatures under the deciduous canopy types were higher than those under the conifer canopy types ($p < 0.0001$ for both the *Thuja-Betula* and the *Abies-Populus* stands) (Table III).

SURVEY OF NATURAL REGENERATION

In the *Thuja-Betula* stands, *T. occidentalis* seedlings and germinants in 1994 and 1995 occurred in overwhelmingly larger numbers on decayed wood under the *Thuja*
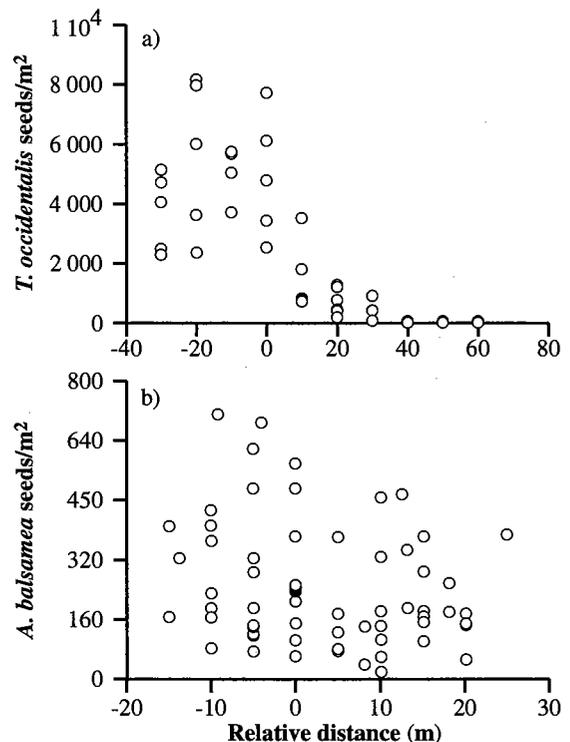

FIGURE 2. Conifer seed dispersal in two mixed-species forest types (fall 1994). Distance is relative to the conifer-deciduous border. Negative numbers are trap positions along portions of transects located under the conifer canopy types. Points represent individual seed traps. a) Relative distance and *T. occidentalis* seed dispersal were strongly correlated ($p < 0.0001$) in the *Thuja-Betula* stand. The equation for decline in number of dispersed seeds with distance from the conifer patch interior was: $\sqrt{\text{number of seeds/m}^2} = 46.44 - 0.76 *$ (distance in meters); $r^2 = 0.87$. b) Trend with distance was not significant ($p < 0.10$) for *A. balsamea* seed dispersal in the *Abies-Populus* stand: $y = 258.56 - 398.95 *$ (distance in meters); $r^2 = 0.28$.

canopy than anywhere else (Figure 3a,b,c). However, the ratios of numbers of *T. occidentalis* germinants (m⁻²)/numbers of seeds (m⁻²) beneath the *Thuja* and the *Betula* canopy types were 1.1×10^{-3} and 1.5×10^{-3}, respectively, indicating

TABLE I. Microfeature aerial coverage, density and other attributes

	Stumps		Mounds		Pits		Logs		Level	
THUJA-BETULA STUDY AREA										
Canopy types[1]	To	Bp	To	Bp	To	Bp	To	Bp	To	Bp
% of forest floor	1.4 (0.3)*	1.1 (0.8)	17.2 (3.2)*	14.4 (2.5)*	2.9 (0.8)#	5.7 (1.0)#	7.7 (1.0)*	7.1 (1.8)*	71.3 (4.0)	72.4 (3.8)
Density, no./100 m²	9.8 (0.9)#*	6.8 (0.7)#*	14.6 (1.3)*	11.5 (1.8)*	6.8 (0.9)	7.7 (0.8)	24.1(2.2)	18.5 (3.0)		
Mean size, m²	0.2 (0.0)	0.3 (0.1)	1.9 (0.4)	2.2 (0.3)	0.6 (0.1)	0.8 (0.2)*	0.8 (0.2)*	0.7 (0.1)*		
Mean decay class[2]	2.7 (0.1)	2.8 (0.2)	3.3 (0.2)	3.5 (0.2)	3.7 (0.1)	3.5 (0.1)	1.9 (0.1)	1.8 (0.1)		
ABIES-POPULUS STUDY AREA										
Canopy types[1]	Ab	Pt	Ab	Pt	Ab	Pt	Ab	Pt	Ab	Pt
% of forest floor	0.1 (0.1)*	0.2 (0.0)	6.0 (1.4)*	2.6 (0.8)*	2.2 (0.6)	1.3 (0.4)	3.2 (0.6)*	1.9 (0.3)*	88.2 (1.9)	94.1 (1.0)
Density, no./100 m²	2.6 (0.4)*	2.3 (0.7)*	5.1 (0.8)*	3.3 (0.6)*	5.6 (0.9)	5.3 (1.1)	19.6 (2.0)#	12.5 (1.8)#		
Mean size, m²	0.1 (0.0)	0.0 (0.0)	1.7 (0.4)	1.6 (0.6)	0.4 (0.1)	0.3 (0.1)*	0.4 (0.1)*	0.4 (0.1)*		
Mean decay class[2]	2.9 (0.1)	2.8 (0.2)	4.0 (0.0)	4.0 (0.0)	3.6 (0.3)	4.0 (0.0)	2.0 (0.1)	1.9 (0.1)		

[1]Canopy types: *Thuja occidentalis* (To), *Betula papyrifera* (Bp), *Abies balsamea* (Ab), *Populus tremuloides* (Pt). In *Thuja-Betula* stands, substrate moisture levels differed greatly ($p = 0.01$) between the two stands. TB1: *Betula* = 39.3 (4), *Thuja* = 55.1 (4); TB2: *Betula* = 64.6 (3); *Thuja* =52.5(5). There were no site differences in soil moisture for *Abies-Populus* stands. 1 SE shown in parentheses.
[2]Estimated microsite age (see Material and methods).
#Differences between canopy types within study area ($p < 0.05$).
*Differences between like canopy types (*i.e.*, *Thuja* versus *Abies* and *Betula* versus *Populus*) at each study area ($p < 0.05$).
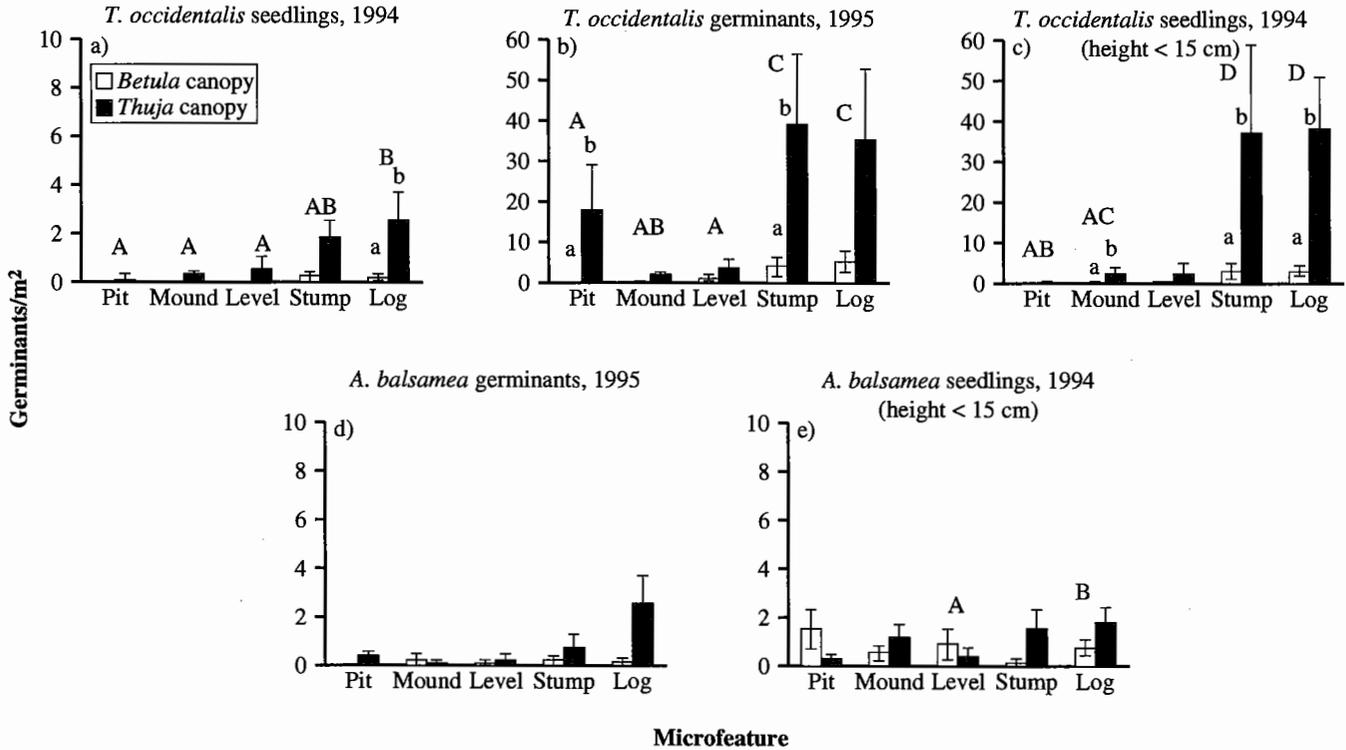
FIGURE 3. Distribution patterns on different microfeatures and under different canopy types in the *Thuja-Betula* stands. In a), b) and c), germinant and seedling densities were greater under the conifer canopy type than the deciduous canopy type when microfeatures were pooled ($p < 0.01$; Wilcoxon). Bars with different letters differed significantly ($p < 0.05$; Wilcoxon). Capital letters indicate a difference between microfeatures when canopies were pooled, and lowercase letters indicate differences between microfeatures beneath different canopy types.

that seed rain differences largely drove patch differences in numbers of germinants.

In addition to the tremendous effects of canopy and substrate, *T. occidentalis* seedling and germinant distribution also varied with a number of environmental variables (Table IV). High seedling densities of *T. occidentalis* occurred on microfeatures with higher soil moisture ($p = 0.0009$), except in the case of pits where moisture was high, but seedling densities were lower than for mounds, stumps, and logs (Figure 3c; Tables III and IV). *T. occidentalis* seedlings also grew predominantly on microfeatures with

TABLE II. Percent aerial coverage of wood[1] in different decay classes in two *Abies-Populus* stands and two *Thuja-Betula* stands

Decay class[2]	Canopy type			
	Thuja	*Betula*	*Abies*	*Populus*
0	1.2 (0.5)	2.6 (1.2)		
1	0.8 (0.2)	1.2 (0.5)	1.9 (0.4)##	0.6 (0.1)##
2	3.0 (0.9)*	2.2 (1.0)	0.5 (0.1)*	0.7 (0.1)
3	2.3 (0.4)# **	1.7 (0.5)# *	1.0 (0.4)**	0.8 (0.2) *

[1] Log and stump data are combined, and 1 SE is shown in parentheses.
[2] See Methods (survey of microtopography) for decay class descriptions.
Differences between canopy types within study areas ($p < 0.10$)
Differences between canopy types within study areas ($p < 0.01$)
* Differences between like (*e.g., Thuja versus Abies*) canopy types across study areas ($p < 0.05$)
** Differences between like (*e.g., Thuja versus Abies*) canopy types across study areas ($p < 0.01$)
Percentages represent the area of forest floor occupied by wood in each decay class.

high substrate temperatures ($p < 0.0001$; Table IV). Although larger numbers of *T. occidentalis* seedlings consistently occurred under the cooler *Thuja* canopy type, especially high numbers grew on the warmer microfeatures, *i.e.*, stumps and logs (Figure 3c; Table III). Germinant densities of *T. occidentalis* were higher on microfeatures with thin litter layers (1994), low herbaceous cover (1995), and a high percent cover of low shrubs (1995) ($p = 0.004$, $p < 0.0001$, $p = 0.001$, respectively; Table IV).

In the *Thuja-Betula* stands, differences in canopy type and microfeature were not associated with *A. balsamea* germinant densities, but seedling densities of *A. balsamea* were higher on logs than on level microfeatures (Figure 3d,e). In the *Abies-Populus* stands, more *A. balsamea* germinants occurred under the *Abies* canopy type than under the *Populus* canopy type, especially on stumps (Figure 4a). Seedling densities of *A. balsamea* differed among some microfeatures in the *Abies-Populus* stands regardless of canopy type (Figure 4b). The ratios of numbers of *A. balsamea* germinants (m^{-2})/numbers of seeds (m^{-2}) beneath the *Abies* and the *Populus* canopy types were 8.6×10^{-3} and 5.3×10^{-3}, respectively.

Although canopy and substrate effects on *A. balsamea* in the *Thuja-Betula* stands were not as pronounced as for *T. occidentalis*, *A. balsamea* distribution did appear to vary with a few environmental variables. The 1995 germinant densities of *A. balsamea* were higher on warmer microfeatures in the *Thuja-Betula* stands ($p = 0.006$; Table IV) but higher on cooler microfeatures in the *Abies-Populus* stands

TABLE III. Seedbed characteristics of pit, mound, level, and rotten wood microfeatures in two *Abies-Populus* and two *Thuja-Betula* stands*

	Substrate moisture (%)		Substrate temperature (°C)		Litter depth (cm)	
THUJA-BETULA STUDY AREA						
Canopy type	*Thuja*	*Betula*	*Thuja*	*Betula*	*Thuja*	*Betula*
Microfeature						
Mound	36 (5)^a	44 (7)	11.0 (0.5)^{ab}	12.4 (0.3)	1.2 (0.2)^a	1.3 (0.2)^a
Pit	61 (7)^{ab}	63 (7)	8.3 (1.0)^a	9.9 (0.1)	2.5 (0.2)^b	2.7 (0.1)^b
Level	61 (4)^b	44 (7)	8.8 (1.0)^a	10.4 (0.3)	1.7 (0.1)^a	1.5 (0.2)^a
Stump	49 (6)^{ab}	43 (8)	13.0 (0.6)^b	12.9 (0.6)		
Log	63 (5)^b	56 (8)	12.5 (0.6)^b	10.1 (0.4)		
Canopy mean	54 (3)	50 (3)	10.8 (0.2)$^\#$	12.1 (0.2)$^\#$	1.7 (0.2)	1.7 (0.2)
ABIES-POPULUS STUDY AREA						
Canopy type	*Abies*	*Populus*	*Abies*	*Populus*	*Abies*	*Populus*
Microfeature						
Mound	42 (5)^a	43 (6)^a	9.3 (0.4)^a	11.0 (0.3)^a	1.7 (0.2)^a	2.0 (0.2)
Pit	55 (7)^{ab}	52 (6)^{ab}	8.9 (0.4)^a	10.0 (0.3)^a	2.7 (0.3)^b	2.1 (0.1)
Level	51 (5)^{ac}	52 (6)^a	8.7 (0.3)^a	10.8 (0.3)^a	1.7 (0.1)^a	2.1 (0.2)
Stump	72 (1)^{bc}	77 (4)^{ab}	13.5 (0.4)^b	14.2 (0.6)^b		
Log	73 (5)^b	77 (3)^b	11.5 (0.7)^b	12.6 (0.5)^b		
Canopy mean	58 (0.3)	56 (0.3)	10.1 (0.2)$^\#$	11.3 (0.3)$^\#$	2.0 (0.1)	2.0 (0.1)

*All data were gathered at the time of germination (June 1995). Most recent rainfall was 7 days prior (60 mm) for *Thuja-Betula* stands and 2 days prior (157 mm) for *Abies-Populus* stands. Data shown for % soil moisture are % dry mass and (1 SE). Data shown for soil temperature and litter depth are means (3 replicates) and (1 SE). Superscripts represent significant differences among microfeatures beneath the listed canopy type ($p < 0.05$; Tukey-Kramer HSD).
$^\#$Differences between mean values under different canopy types ($p < 0.01$).

($p = 0.05$ (not shown in Table IV)). *A. balsamea* seedling densities in the *Thuja-Betula* stands were higher on microfeatures with a thin litter layer and a high percent cover of low shrubs ($p = 0.008$, $p = 0.007$, respectively; Table IV). The number of *A. balsamea* germinants surveyed in 1994 was insufficient to perform analyses (data not shown).

Evaluating the implications of seedling densities for stand regeneration required scaling by the percent aerial coverage of each of these features. For example, low seedling and germinant densities of *T. occidentalis* occurred on level ground, but this microfeature occupied over 70% of the forest floor. As a result, total numbers of *T. occidentalis* occurring on level ground were large (Figure 5a). In contrast, high seedling and germinant densities of *T. occidentalis* occurred on logs, but logs occupied only 7% of the forest floor. The resulting total of *T. occidentalis* seedlings and germinants on logs was comparable to that of level ground (Figure 5a). Total numbers of *T. occidentalis* germinants and seedlings on mounds, pits, and stumps were small in comparison. The proportion of germinants and seedlings occurring on stumps, however, was approximately 7 times greater than the proportion of the forest floor occupied by these features (Figure 5a).

Relatively high densities of *A. balsamea* seedlings

occurred on level ground, which also occupied the largest percentage of the forest floor (Figures 4b, 5c). As a result, the majority of germinants and seedlings occurred on level microfeatures.

Discussion

SEED AVAILABILITY

Conifer seed availability differed beneath the different canopy types, and appeared to be a strongly positive feedback for densities of conifer germinants beneath conifer and deciduous canopy types at both study sites. *T. occidentalis* germinant:seed ratios were equal or greater under the *Betula* canopy than under the *Thuja* canopy type, suggesting that ten-fold higher *T. occidentalis* seed availability in the *Thuja* patches was largely responsible for higher densities of germinants under the *Thuja* canopy type in 1995. This contrasts with the findings of Bartlett, Reader & Larson (1991), who reported that in an old-growth *Thuja occidentalis* forest along the Niagara Escarpment in Ontario, a sharp boundary between adjacent *Thuja* and *Acer* patches, is maintained by litter differences rather than seed dispersal limitations. Our seed:germinant ratios also indicated that higher *A. balsamea* seed availability under the *Abies* canopy type may have led to larger numbers of *A. balsamea* germinants under the

TABLE IV. Significant results for Poisson regressions of conifer seedlings and germinants on environmental variables in the *Thuja-Betula* stands

	Substrate moisture	Substrate temperature	Litter depth	Herbaceous cover	Low shrub cover	Tall shrub cover
T. occidentalis germinants,1994	0	0	-	0	0	0
T. occidentalis germinants,1995	0	0	0	-	+	0
T. occidentalis seedlings	+	+	0	0	0	0
A. balsamea germinants,1995	0	-	0	0	0	0
A. balsamea seedlings	0	0	-	0	+	0

+, -, and 0 are positive, negative and neutral associations, respectively, between conifer regeneration and environmental variables. The only environmental variable that played a role in *A. balsamea* distribution in the *Abies-Populus* stands was a negative association with substrate temperature for germinants, not shown here.
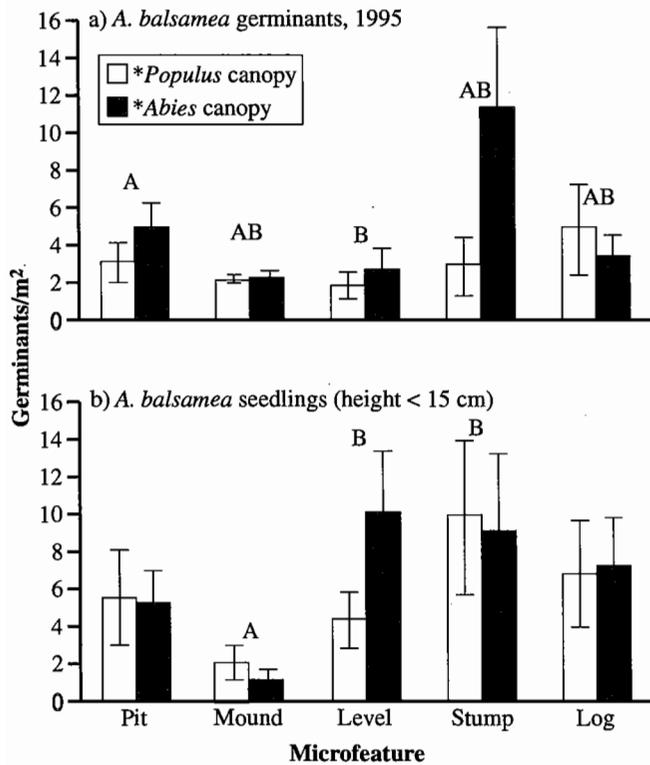
FIGURE 4. Distribution patterns on different microfeatures and under different canopy types in the *Abies-Populus* stands for *A. balsamea* germinants, 1995 (a) and *A. balsamea* established seedlings, not including germinants, 1994 (b). Bars represent mean numbers of seedlings/m². Error bars are ± 1 SE. * signifies a difference between germinant densities beneath the two canopy types (microfeatures pooled) ($p < 0.05$; Wilcoxon). Bars with different letters differed significantly when canopies were pooled ($p < 0.05$; Wilcoxon two-sample test).
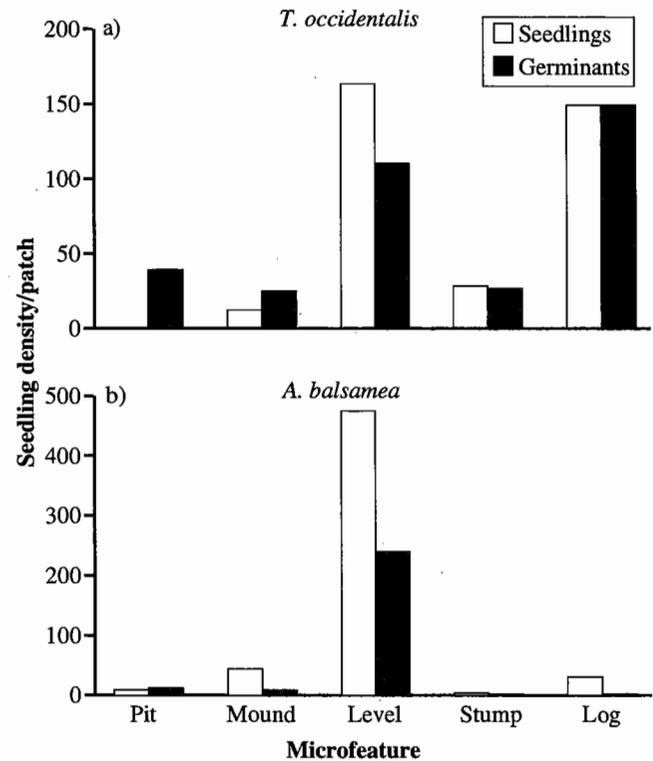

FIGURE 5. Seedling densities/"patch" (arbitrarily scaled as 100 m²) calculated from % aerial cover and mean seedling density/m² for each microfeature type (*e.g.*, *T. occidentalis* seedlings on level ground: (2.3/m²) * (71.8 m²/100 m²) = 165.1 seedlings on level ground/100 m²). Data are for each microfeature, and added together represent all seedlings occurring on all features within 100m². Seedling distributions on microfeatures follow similar patterns beneath both deciduous and evergreen canopy types in both forest types, and here are lumped together. a) *T. occidentalis* in the *Thuja-Betula* stands. b) *A. balsamea* seedlings in the *Abies-Populus* stands.

Abies canopy type than under the *Populus* canopy type in 1995, although the trend was not as strong as for *T. occidentalis*. Likewise, larger numbers of germinants of both species in 1995 than in 1994 may have resulted from a better seed crop in 1994 than in 1993. Seed rain varies interannually for both species, with mast seed crops occurring every 3-5 years (Frank, 1990; Johnston, 1990).

The correlation of distance from conifer patch interior with conifer seed rain in the *Thuja-Betula* stands but not in the *Abies-Populus* stands may be explained in part by differences in stand configuration. Feedback within larger patches may be more pronounced, accounting for an uneven distribution of *T. occidentalis* seeds beneath the two canopy types in the *Thuja-Betula* stands. Co-mingling of canopy types on a finer spatial scale in the *Abies-Populus* may have resulted in a blurring of conditions beneath the two canopy types, including spatial patterns of seed distribution.

MICROFEATURES AND TREE REGENERATION

Microtopographic heterogeneity appeared to interact with canopy feedback. The dramatically higher numbers of *T. occidentalis* germinants and seedlings on decayed wood than on other microfeatures may have resulted from a variety of processes. Variation in surface roughness among microfeatures and seed size may lead to differential trapping of

seeds among microfeatures (Johnson & Fryer, 1992). Higher densities of *T. occidentalis* germinants on rough-surfaced decaying wood in both 1994 and 1995 may have simply resulted from higher seed retention by these microfeatures. *A. balsamea* seeds may have been trapped less effectively by these microfeatures since its larger seeds are less likely to lodge in small crevices.

If a microfeature retains seeds, the next question is whether it provides the conditions necessary for germination. Decayed wood may both effectively retain seeds and provide good seedbed conditions. High densities of *T. occidentalis* germinants on decaying wood were consistent with other studies (McCullough, 1948; Scott, 1984). Although climate and *T. occidentalis* total seed rain can vary interannually, germinant distribution patterns observed in the present two-year study are likely to occur in other years, except possibly under prolonged drought conditions. In 1994, total precipitation from June-August in the *Thuja-Betula* stands and the *Abies-Populus* stands was 261 mm (Split Rock Lighthouse State Park, Minnesota Department of Natural Resources and the Minnesota Historical Society), and 329 mm (Cloquet Forestry Center, University of Minnesota), respectively, compared with 30-year averages of 285 mm and 318 mm (Midwestern Climate Center; Illinois State Water Survey, Champaign, Illinois). In the

present study, percent substrate moisture and temperature for decayed wood were generally higher than for other microfeatures, but moisture retention may decrease with time since most recent precipitation. Perhaps these characteristics also create good conditions for seed germination. Litter cover was sparse on stumps and logs, one of the conditions favorable for conifer germination (Cornett, 1996). Harmon & Franklin (1989) argue that if logs are able to shed litter, they also can shed seeds. Seeds, however, can become lodged in smaller crevices than the average leaf and, therefore, may not be shed as readily as leaves.

Just as surfaces that trap seeds effectively do not necessarily provide ideal germination conditions, good seedbeds do not ensure future seedling growth and survival (Harmon & Franklin, 1989; Ohlson & Zackrisson, 1992). As an example of different germination and survival rates on the same microfeature, high densities of *T. occidentalis* germinants occurred in pits in 1995. Pits provided more favorable early germination conditions than level ground or mounds for *T. occidentalis* in the unusually dry June of 1995. Despite higher germination rates of *T. occidentalis* in pits, low densities of established seedlings indicated that few seedlings survived in pits in previous years.

Seedling densities in pits may be low for a variety of reasons that may fluctuate interannually. For example, flooding in years of heavy precipitation and accumulation of a thick litter layer may preclude seedling survival in pits (Friesner & Potzger, 1932; Sydes & Grime, 1981). In some years, frost may also be more likely to damage seedlings growing in pits, since pits may function as small frost pockets (Clements, 1963). In the present study, when regular rainfall resumed in July, pits at the *Thuja-Betula* study area filled with water, submerging newly-germinated seedlings. Virtually all 1995 germinants in pits had died by the end of the growing season. It is worth noting that if the drought had persisted throughout the summer, germinants might have survived at higher rates in cool, moist pits than on decayed wood. The occurrence of high *T. occidentalis* germinant densities in pits in addition to decayed wood suggested that germination may be a less restricted process than first year establishment. This pattern contrasted with regeneration in a hemlock-hardwood stand in New York, where hemlock germination is more restricted than establishment by such variables as type and depth of litter (Collins, 1990).

The microenvironment created by decayed wood, in contrast to that of pits, may generally be favorable for both germination and survival. Although interannual fluctuations in precipitation and temperature may lead to differential seedling survival rates among microfeatures, continued survival on decayed wood seems to be higher than on other microfeatures. Among the advantages conferred by decayed wood for seedling growth and survival are the accumulation of bacterially fixed nitrogen (Sharp & Millbank, 1973; Maser & Trappe, 1984), high mycorrhizal activity (Harvey, Larsen & Jurgensen, 1976; 1979), lower herbaceous cover, and higher water content.

Densities of *A. balsamea* seedlings also varied more with microfeatures than did germinants. In the *Thuja-Betula* stands, densities of *A. balsamea* germinants did not differ among microfeatures but young seedlings occurred in higher densities on logs, which had virtually no litter cover, than on level microfeatures. The negative correlation between seedling densities of *A. balsamea* and litter depth was consistent with that observed in a manipulated field experiment (Cornett, 1996). Although higher germinant densities on stumps may have occurred, stumps were rare in the *Abies-Populus* stands resulting in small, uneven sample sizes, high measures of error, and a lack of statistical significance. A more distinct pattern emerged for established seedling densities, which were consistently higher on raised microfeatures than in pits. The distinction between germinant and seedling patterns for *A. balsamea* supported Clements' (1963) differential mortality hypothesis: Distribution patterns of *A. balsamea* seedlings are initiated during the first and second summers of seedling development and result from higher mortality in pits rather than higher germination success on mounds.

MICROFEATURE AVAILABILITY

Heterogeneity of microtopography not only interacted with canopy feedbacks as in the previous section, but also resulted from feedbacks. Microfeatures other than level ground covered a greater area in the *Thuja-Betula* stands ($\approx$ 30%) than in the *Abies-Populus* stands ($\approx$ 9%), most notably wood in decay class three. Published estimates for microfeature aerial coverage in temperate forests range from 6% to 42% of the forest floor (Lyford & Maclean, 1966; Falinski, 1978; Webb, 1988).

Signs of logging (*i.e.*, cut stumps) beneath both the *Thuja* and the *Betula* canopy types suggested that the deposition of logs on the forest floor may have been reduced by the removal of mature trees (McFee & Stone, 1966; Falinski, 1978; Alverson, Kuhlman & Waller, 1994), resulting in comparable aerial coverage of logs (decay classes lumped) beneath the two canopy types. The higher proportion of decay class 3 logs under the *Thuja* canopy type than the *Betula*, however, may be of great importance, since this is the relevant decay class for the regeneration of many species (Holcombe, 1976; Christy & Mack, 1984). Since patches within *Abies-Populus* stands originated at around the same time (*i.e.*, within the past 60 years) and were intermixed on a small spatial scale, the similarity of aerial coverage under the two canopy types was not surprising.

The interaction between feedbacks and microsite heterogeneity has a different implication for scales larger than individual microfeatures (*e.g.*, at stand rather than stump level). Numbers of *T. occidentalis* germinants and seedlings per stand on log and level microfeatures were comparable despite the discrepancy in percent aerial coverage between the two microfeatures. Similarly, in a *Pinus-Abies* forest (Itasca State Park, Minnesota) seedling densities are over five-fold higher on stumps and two-fold higher on logs than on level ground per surface area of microfeature (Webb, 1988). Calculated for the stand level, however, the situation nearly reverses, with the number of seedlings on level ground within a stand over four times higher than on decaying logs and around seven times higher than on stumps, based on the percent availability of these microfeatures (calculated from Webb, 1988). In the above forest types, some microfeatures were more important than others as

safe sites for seed germination and seedling establishment, but they can only contribute to the total regeneration pool to the extent that canopy feedbacks supply them (e.g., percent total forest floor area occupied). In contrast, total seedlings and germinants of A. balsamea in the Abies-Populus stands occurred on microfeatures in proportion to their relative availability instead of specializing on a particular type of microfeature. These results are consistent with those of Holcombe (1976), who found that A. balsamea seedlings are distributed randomly irrespective of microtopography.

FUTURE STAND DEVELOPMENT

Together, canopy feedback and forest floor heterogeneity may determine the composition of advance woody regeneration. The implications of feedback and microsite heterogeneity for future stand composition requires a detailed examination. High densities of T. occidentalis seedlings and germinants occurred on decaying logs but the seedlings were concentrated on a few logs. As seedlings grow they will begin to compete with each other or die for other reasons. High seedling densities on logs are reduced rapidly by self-thinning (Harmon & Franklin, 1989). In addition, few seedlings survive bark and wood fragmentation and competition, resulting in dramatic reductions in numbers of trees reaching maturity on these microfeatures (Harmon & Franklin, 1989). The currently higher stump densities under the Thuja canopy type than the Betula may eventually contribute to higher rates of regeneration under the Thuja canopy type. If one T. occidentalis tree per stump grows to maturity, future tree density may be affected more by stump density than by aerial coverage of stumps.

Seedlings occurring on level microfeatures will experience lower levels of intraspecies competition in the first few years, because they occur at lower densities, and will not be subjected to bark fragmentation. Level ground does present a number of other hazards, however, such as competition with other vegetation or litter accumulation. Nonetheless, recruitment of trees from soil-established seedlings may be greater than indicated by proportions of seedlings occurring on different seedbeds (Harmon & Franklin, 1989). In fact, Scott (1984) asserts that the T. occidentalis trees surviving to maturity in a Michigan old-growth forest germinated on level ground rather than stumps and logs.

Although A. balsamea seedling densities in the Thuja-Betula stands were comparable to those of the Abies-Populus stands, they were low in both forest types relative to T. occidentalis densities beneath the Thuja canopy type. In some cases, after Thuja stands are opened by disturbance or are subjected to intense browsing by white-tailed deer, Abies or swamp hardwoods replace Thuja (Johnston, 1972; 1990). Although T. occidentalis seedlings occurred in much higher densities than A. balsamea under the Thuja canopy type, differential mortality rates (resulting from deer browsing or other causes) between two species may lead to the eventual dominance of a species with initially low numbers of germinants (Davis, Puttmann & Perala, unpubl.).

Conclusions

The effects of canopy feedback and microsite heterogeneity on conifer regeneration differed for the two study species and forest types. The distribution of T. occidentalis was more restricted than that of A. balsamea. Positive canopy feedbacks played an important role in T. occidentalis regeneration. Such feedbacks included higher T. occidentalis seed input, alteration of seedbed heterogeneity, and modification of microclimate. T. occidentalis was largely restricted to areas beneath the Thuja canopy type during both the germination and establishment phases. A. balsamea regeneration was less a part of a feedback loop, occurring in somewhat higher densities beneath the conifer canopy types at the germination stage, but not during establishment. Heterogeneity of microfeatures was an important aspect of feedback processes. Although T. occidentalis seedlings were concentrated on decayed wood, these microfeatures occupied only a small percentage of the forest floor beneath both the Thuja and the Betula canopy types. In forests where for historical or other reasons canopies have not supplied adequate seedbeds to the forest floor, species with less-specialized regeneration niches may interrupt the positive feedback, resulting in a switch to a new forest type.

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Development of Tree and Understory Vegetation in Young Douglas-Fir Plantations in Western Oregon

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ABSTRACT: *The prevalence of young even-aged Douglas-fir (*Pseudotsuga menziesii*) stands in Oregon and Washington has led to concerns about a landscape being dominated by stands in the stem exclusion phase. In this context, our study documented the development of two aspects important for the diversity of plant and wildlife habitat: tree characteristics and understory vegetation. Using a chronosequence approach, we measured conditions in 39 plantations ranging from 6 to 20 years. Results confirmed intuitive trends, but the quantification indicated that some of these trends develop earlier than commonly assumed. Tree growth in young stands was positively related to stand density, but this trend reversed fairly early. Crown characteristics were influenced very early by stand density, indicating that maintaining a long-lived crown in typical plantations can only be accomplished by lowering stand density through precommercial thinning. Understory herb cover was reduced throughout time, while shrub cover increased. Species compositions were quite complex, with an initial strong presence of invader species and later dominance of species usually associated with mature forests; however, there were many exceptions and early successional species were still present after 20 years. The study showed that this early stage is very complex, that the dynamics vary for different characteristics, and that a finer resolution of the stand initiation stage may be warranted for plantations. West. J. Appl. For. 21(2):94–101.*

Key Words: Density management, stand initiation phase, crown characteristics.

Forest managers are now challenged with creating a diversity of forest stand structures while also producing revenue, such as in the recent adoption of the Oregon Department of Forestry's Northwest Oregon State Forests Management Plan (Oregon Department of Forestry 2001). A diversity of stand structures is considered important to maintain the diversity of species and ecosystem functions (Spies et al. 1988, Oliver and Larson 1996). As a result of past harvesting practices in the Pacific Northwest, the reduced acreage in late-successional structures and the associated dominance of early successional stand structures (analogous to stem exclusion phase sensu Oliver and Larson 1996) have received recent attention (Kohm and Franklin

1997). This trend is of special concern because the stem exclusion phase is regarded as having less diversity in stand structures and habitats (Spies et al. 1988) than late successional stages.

Analysis of early growth rates of trees in old-growth stands in the Oregon Coast Range indicated that these stands may have initiated at lower densities than commonly found in current plantations and may have never gone through a classic stem exclusion phase (Poage and Tappeiner 2002, Tappeiner et al. 1997). These findings raised the question whether the current, dense plantations will develop efficiently into forests that provide late successional habitat. As a consequence, a number of studies have been initiated to investigate whether density reductions in dense plantations can accelerate the development of desirable stand characteristics, such as a diversity of understory vegetation or multiple crown layers. Most of these studies focused on the later stages of the stem exclusion stage, when trees are of sufficient size to make thinnings commercially attractive (for a listing of studies, see Monserud 2002). Little work however, has been done to investigate whether negative aspects of stem exclusion can be prevented or

lessened through density management in the regeneration establishment phase.

The objective of this study was to characterize development of stand structure during the transition from the regeneration to the stem exclusion phase in young Douglas-fir plantations. Specifically, we wanted to quantify how development of tree and crown characteristics and understory vegetation was influenced by stand density during the transition. This information is crucial to evaluate whether preventing the loss of valuable structural components through early management is a viable option for forest managers. It may provide an alternative to currently common practices that focus on reintroducing these structural components through thinnings after they had been lost during the stem exclusion phase.

Methods

Study Area

Study stands were located in three Oregon Department of Forestry districts (Astoria, Forest Grove, and Philomath) in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973) in the middle to northern part of the Oregon Coast Range. Dominant tree species in this zone include: Douglas-fir, western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). The Coast Range has a maritime climate characterized by mild, wet winters and relatively dry summers. Mean temperatures range from 4° C in January to 16° C in July and annual precipitation, mostly occurring November through March, ranges between 115–255 cm. Soils differ between districts, but in general the soils in the Coast Range are derived from sandstones, siltstones, weathered basalts, and volcanic breccias and range from deep, rock-free materials to shallow, stony profiles (Oregon Department of Forestry 2001).

Study Layout

Using a chronosequence approach, Douglas-fir plantations from 6 to 20 years were selected from a list of candidate stands. Selection criteria included typical stand establishment procedures, average site quality, no major disease problems, and no release treatment in the previous 2 years. To ensure coverage of density gradients, we laid out three transects in each stand with each transect consisting of three areas (*n* = nine plots per stand) in close vicinity, i.e., with similar slope and aspect, that differed in overstory densities. The three overstory densities on each transect included a low (open gap, typically one to three crop trees/plot), medium (transition or low density, typically

three to four crop trees/plot), and high (matrix or fully stocked, typically four to six crop trees/plot) density condition. Within this constraint, a 5-m radius plot was located randomly in each overstory density condition, resulting in a total of three plots per transect and nine plots in each stand. Crop trees included all planted trees that achieved locally dominant positions. To minimize the effect of other factors, areas were not selected if they were infected with rot pockets, part of an old skid trail or landing system, or had existing hardwoods that predated crop trees.

Tree and Crown Measurements

For all trees greater than 1.4 m in height and 2.5 cm in dbh we measured species, dbh, current total height in 2002, 2001 height, 2000 height, height to base of live crown, and crown radius. We also measured height, length, diameter, and angle of the lowest live branch for crop trees.

Understory Vegetation Measurements

Within each 5-m radius tree plot, four 1-m radius subplots were placed 2.5 m off tree plot center in the cardinal directions. In each subplot, percent cover was estimated to the closest 10% (also <1 and 1 to 5% noted) for all forbs, fern, grass, sedge, moss, lichen, shrub, and tree species. In addition, we estimated the cover of bare ground, rock, stumps, downed wood, and needles. All vegetation was identified to species except moss, lichen, grass, and sedges.

Data Analysis

An analysis of covariance test (data not shown) showed significant differences among districts. We considered these results an artifact of several factors, which cannot be separated (e.g., location, especially topography and history, and differences in recent silvicultural practices such as planting densities and site preparation treatments; see Table 1) and therefore analyzed the districts separately. The distinction of gaps, transitions, and matrices was used for the purpose of plot installation only. In the analysis, we used actual densities as independent variables. More specifically, we used total basal area, which accounts for numbers and sizes of all trees as a representation of stand density. Number of trees was not a proper reflection of the intensity of competition within a plot, because the number of trees in plots with only large crop trees does not have the same ecological influence in plots that contained small hardwoods (see Table 1).

To account for the potential correlation between plots on transects and within stands, we used a mixed model that included planted Douglas-fir basal area, site index (King

Table 1. Summary information for study sites. Plantation ages refer to years since planting and site index (SI) is measured in meters at 50 years (King 1966). Crop trees are limited to planted seedlings, while total density includes crop trees and conifer and hardwood natural regeneration.

District	Age (years)	SI (m)	Elevation (m)	Site prep	Crop tree density (tpha)			Total tree density (tpha)		
					Gap	Transition	Matrix	Gap	Transition	Matrix
Astoria	6–20	37–43	195–615	a, b, c, d*	127–637	127–892	127–1656	127–4076	127–3439	127–2166
Forest Grove	7–18	32–40	380–860	b	127–764	255–1019	382–1529	127–6497	255–2548	382–3185
Philomath	6–18	40–43	200–495	a, b, c, e	127–764	255–1019	637–1401	127–9809	637–7134	637–3822

*a = slash and burn, b = broadcast burn, c = chemical site preparation, d = forage seeding, e = trapping.

1966), and age as main effect terms (fixed factor), basal area × age interaction, and stand identification (id), transect within stand id as random factors. Nonsignificant parameters were dropped and the final models only contained significant parameters. Means for tree and crown characteristics were computed and understory vegetation subplots averaged for each tree plot before analysis. Percent cumulative cover for forbs and shrubs was also calculated by adding up the percentage cover of individual species to account for multiple layers of species in a plot. Response variables were assessed for agreement with statistical assumptions (i.e., normality and homoscedasticity of residuals). All response variables were log transformed, except for forb and shrub cover in which a logit transformation was used (Sabin and Stafford 1990).

To analyze the understory vegetation (forbs and shrubs) further, nonmetric multidimensional scaling was used to ordinate plots and to assess overall gradients in vegetation community composition and their relationships with environmental variables. We ordinated vegetation community data from 140, 114, and 87 plots, in Astoria, Forest Grove, and Philomath, respectively. Species present in <5% of the plots were removed from the analysis. A multivariate outlier analysis was run for each district and analysis of all 140 plots in Astoria revealed one potential outlier with a SD three times greater than the 2.0 cutoff. Unlike other plots, this particular plot had zero forb species. After running the analysis with and without the outlier we concluded that the outlier was influential in the ordination and disrupted pat-

terns in the other points and was therefore excluded from further analyses (McCune and Grace 2002). Sørensen distance was used with the Slow and Thorough autopilot mode in PC-ORD 4.0 [40 runs of 400 iterations (Kruskal 1964, Mather 1976)]. The ordination was rotated to maximize the correlation of basal area in Philomath and Astoria and elevation in Forest Grove with one axis. We used coefficient of correlation to assess relationships with species abundance and environmental variables with the ordination axes and for presentation in the results chose a cutoff of $R^2 \geq 0.3$.

Results and Discussion

Tree and Crown Characteristics

The study was not designed to document average stand conditions, but to document conditions in areas with a range of stand densities. Thus, density and species composition of planted trees and natural regeneration as well as understory vegetation are not representative for plantations. Instead, they represent the specific spots selected for measurement. It is important to note that naturally regenerated conifers and hardwoods were concentrated in plots with low crop tree densities and not evenly distributed throughout the stand. Mean sizes of planted conifers and natural conifer regeneration and hardwoods were calculated for each plot and averaged by age in Table 2. The lack of significance of site index (Table 3) in all models is no indication that site quality did not affect tree and crown characteristics; instead, is an artifact of the selection criteria, which aimed for similar site conditions in all stands. Some coefficients such

Table 2. Mean dbh (cm) and height (m) of planted conifers and natural conifer and hardwood regeneration averaged across plots (SD in parentheses). $N = 9$, except for ages with multiple stands ($n = 18$).

| | Age (years) | Planted conifer | | Natural regenerated conifer | | Natural regenerated hardwood | |
		dbh	ht	dbh	ht	dbh	ht
Astoria	6	3.2 (0.78)	3.2 (0.38)			3.9 (0.85)	4.4 (0.75)
	7*	5.0 (1.40)	4.1 (0.78)			4.0 (1.00)	4.5 (0.64)
	8*	7.9 (2.39)	5.3 (1.06)	3.1 (0.64)	3.3 (0.59)	5.6 (1.16)	5.8 (2.69)
	9	9.0 (2.12)	6.2 (1.08)	3.1 (0.35)	4.2 (0.45)	4.8 (1.98)	5.9 (1.20)
	11*	11.6 (3.46)	8.7 (1.64)	5.0 (2.28)	5.4 (1.76)	6.1 (3.19)	7.4 (1.34)
	13*	14.8 (3.62)	10.4 (2.00)	4.2 (1.78)	5.2 (1.59)	3.9 (2.04)	6.4 (2.30)
	14*	15.4 (3.62)	10.8 (1.49)	3.8 (1.04)	4.7 (1.01)	4.7 (2.47)	7.1 (2.86)
	16	19.4 (4.37)	13.0 (2.01)			4.3 (3.54)	7.0 (2.45)
	17	21.0 (4.63)	13.6 (1.61)	7.5 (4.59)	8.2 (3.23)	3.5 (2.04)	6.7 (3.16)
	19	20.9 (5.07)	13.7 (1.63)	5.7 (2.41)	6.3 (2.01)	4.1 (2.65)	5.9 (1.09)
	20	20.8 (5.03)	14.5 (2.22)	7.1 (1.89)	7.1 (1.57)	7.5 (5.28)	9.0 (3.57)
Philomath	6	4.1 (1.19)	3.6 (0.82)			3.0 (0.44)	4.5 (0.59)
	8	7.4 (1.66)	5.8 (1.02)	3.0 (0.45)	3.4 (0.32)	3.5 (0.60)	4.1 (0.62)
	9*	10.4 (2.97)	7.3 (1.50)	3.7 (1.09)	4.1 (0.97)	3.2 (0.71)	4.9 (0.84)
	12*	14.0 (3.68)	9.7 (1.66)	3.6 (1.13)	4.7 (1.72)	4.5 (2.68)	6.3 (2.57)
	13	14.3 (4.54)	9.6 (2.06)	4.8 (–)	6.8 (–)	3.6 (1.30)	5.8 (1.45)
	14	15.3 (4.69)	10.3 (2.18)	5.6 (2.55)	6.9 (3.10)	5.7 (3.06)	7.4 (2.10)
	16	17.3 (5.27)	11.8 (2.35)	7.0 (5.10)	7.4 (1.93)	4.3 (1.93)	6.8 (1.44)
	18	20.4 (5.11)	12.7 (1.84)	5.5 (2.05)	6.8 (1.63)	3.0 (0.44)	5.0 (0.77)
Forest Grove	7*	4.6 (1.41)	3.8 (0.80)				
	9	6.9 (2.05)	5.2 (1.14)	3.5 (0.22)	3.5 (0.40)	2.7 (0.06)	3.3 (0.15)
	11	10.4 (2.32)	7.3 (1.21)	3.9 (1.25)	4.1 (0.91)	3.1 (0.33)	3.5 (0.57)
	12*	7.4 (2.52)	5.6 (1.48)	4.4 (1.83)	4.3 (1.23)		
	13*	8.4 (3.55)	6.3 (2.07)	6.3 (3.13)	5.1 (1.66)	2.7 (–)	4.9 (–)
	14	10.1 (3.23)	6.2 (1.78)	3.4 (0.89)	3.0 (0.32)	3.4 (0.78)	4.6 (–)
	15*	10.2 (3.19)	7.2 (1.88)	4.1 (1.70)	4.2 (1.01)	4.9 (2.46)	6.5 (1.83)
	16	12.5 (4.04)	8.6 (2.24)	4.8 (–)	5.4 (–)	3.8 (1.44)	6.4 (1.43)
	18	13.8 (5.78)	8.9 (2.94)	5.8 (2.29)	5.7 (1.48)		

* Multiple stands.

Table 3. Parameter estimates (SE in parentheses) for equations quantifying impacts of age and stand basal area on (transformed) tree and crown characteristics and understory vegetation.

|	Intercept	Site index	Age (years)	Basal area (m^2/ha)	Age*Basal area
Philomath					
dbh (cm)	0.752 (0.16)		0.123 (0.01)	0.083 (0.01)	−0.005 (0.00)
2002 height growth (m)	−0.138 (0.10)			0.027 (0.01)	−0.001 (0.00)
Crown radius (cm)	4.237 (0.10)		0.079 (0.01)	0.054 (0.01)	−0.003 (0.00)
Height to base of crown (m)	−0.217 (0.17)		0.060 (0.01)	0.014 (0.00)	
Branch diameter (mm)	1.149 (0.16)		0.109 (0.01)	0.069 (0.02)	−0.004 (0.00)
Branch length (cm)	3.614 (0.15)		0.106 (0.01)	0.071 (0.01)	−0.004 (0.00)
Branch height (cm)	1.234 (0.56)		0.187 (0.05)	0.023 (0.01)	
Forb cover (%)	−0.683 (1.08)			−0.044 (0.01)	
Shrub cover (%)	−31.038 (11.30)	0.237 (0.08)		−0.514 (0.07)	0.026 (0.00)
Astoria					
dbh (cm)	0.720 (0.13)		0.126 (0.01)	0.060 (0.01)	−0.003 (0.00)
2002 height growth (m)	−0.360 (0.07)		0.031 (0.01)	0.038 (0.01)	−0.002 (0.00)
Crown radius (cm)	4.149 (0.09)		0.085 (0.01)	0.042 (0.01)	−0.002 (0.00)
Height to base of crown (m)	−0.100 (0.07)			−0.003 (0.01)	0.001 (0.00)
Branch diameter (mm)	1.201 (0.13)		0.095 (0.01)	0.046 (0.01)	−0.002 (0.00)
Branch length (cm)	3.625 (0.11)		0.093 (0.01)	0.043 (0.01)	−0.002 (0.00)
Branch height (cm)	1.635 (0.21)		0.135 (0.02)	0.030 (0.01)	
Forb cover (%)	−0.350 (0.90)			−0.113 (0.01)	
Shrub cover (%)	−16.540 (8.57)	0.152 (0.07)		−0.370 (0.05)	0.015 (0.00)
Forest Grove					
dbh (cm)	0.628 (0.19)		0.106 (0.02)	0.117 (0.03)	−0.006 (0.00)
2002 height growth (m)					
Crown radius (cm)	4.104 (0.08)		0.067 (0.01)	0.075 (0.02)	−0.004 (0.00)
Height to base of crown (m)	0.075 (0.06)		0.016 (0.01)	0.016 (0.00)	
Branch diameter (mm)	1.184 (0.15)		0.086 (0.01)	0.015 (0.01)	
Branch length (cm)	3.568 (0.13)		0.084 (0.01)	0.019 (0.01)	
Branch height (cm)	1.796 (0.38)		0.085 (0.03)		
Forb cover (%)					
Shrub cover (%)	−2.037 (1.39)			−0.077 (0.02)	

as height growth, diameter, and length of lowest live branch, shrub cover, and forb cover were inconsistent across districts (Table 3) and may be random effects or, if real, are possibly related to site conditions and specific area effects.

Our study design does not allow us to calculate the specific timing of the "crossover effect" (Scott et al. 1998, Turnblom and Pittman 2001) because of our choice of basal area. However, the results support the conclusion that the early positive effect of density on height growth, dbh, and crown radius (Figure 1) caused by dense planting is temporary and lost during the canopy closure stage (Scott et al. 1998). Future thinning studies will provide insight as to whether the initial growth benefits can be maintained throughout a rotation, but our data suggest that early density manipulations are necessary to capture the early growth advantage of dense plantations.

The effects of higher densities on crown recession (Figure 1) were already evident fairly early and diameter, length, and height of the lowest live branch were also strongly influenced by stand density throughout time (Note, a positive relationship between density and diameter and length of lowest live branch was found in Forest Grove) (Table 3). Thus, the relationships between crown structure and stand density, i.e., trees in denser stands have shorter crowns and smaller branch diameters (Maguire et al. 1999) is already evident in very young plantations, even though crown radius is not yet negatively influenced by stand density. We documented increased branch mortality that leads to crown recession and loss of the live crown (Maguire et al. 1991) at higher densities already in the youngest

plantations, indicating that on these sites the trends to lower live crown ratios and eventually narrow single-layered canopy structures (Marshall and Curtis 2002) were already established by age 5. Although at this early stage branch sizes are not large enough to affect wood quality, the loss of live crown is critical because it is not easily recovered. Any increase of live crown ratios after thinning is mainly caused by reduced or absent branch mortality in combination with height growth (which, in turn, is fairly insensitive to thinning) (Marshall and Curtis 2002). Although Douglas-fir is able to develop epicormic branches (Bryan and Lanner 1981), the initiation of epicormic branches has been associated with older crowns (Ishii and Ford 2001) or very open conditions around the stems, such as found after intensive pruning in low-density stands (Collier and Turnblom 2001). Consequently, under standard plantation management practices it is unlikely that epicormic branches replace dead branches in these stands as components of vigorous crowns.

Crown and branch size are important stand structural components because they are related to stand growth and vigor, thinning regime (Smith et al. 1997), wood quality (Barbour and Parry 2001), bole form and breakage resistance (Dunham and Cameron 2000, Mitchell 2000), and wildlife and epiphyte habitat (McCune et al. 2000). Although the structural components in the plantations in this study were not necessarily past any critical or threshold stage (Wilson and Oliver 2000), our analysis seems to indicate that crown development is very dynamic at early stages. Desired crown and canopy structure may be developed through early management practices, such as heavy

(a)

(b)
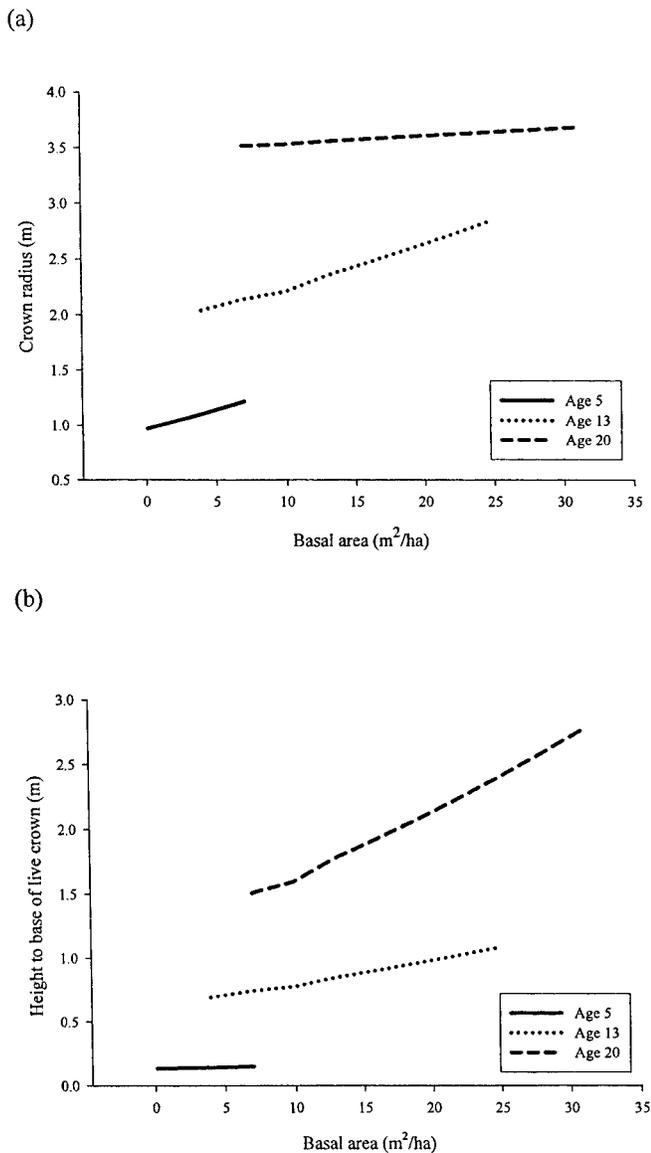
Figure 1.   Fitted regression lines of crown radius (a) and height to base of live crown (b) for plantations in the Astoria district as a function of stand basal area. Lines represent different ages.

precommercial thinning or gap creation (Wilson and Oliver 2000).

Understory Vegetation

Understory vegetation data was recorded in June and July (2003) and quantified as a percent cumulative cover. Across all districts, percent cumulative shrub cover averaged 53% (ranged 0–143%) and forb cover averaged 20% (ranged 0.1–125%). Area of the plots occupied by bare ground, rocks, stumps, downed wood, or needles was also quantified. Percent bare ground varied greatly for each plot, averaging 2% (ranged 0–66%) cover. Studies investigating natural stands (e.g., Poage and Tappeiner 2002, Tappeiner et al. 1997, for further listings see Oliver and Larson 1996) showed long (>30 years) regeneration periods, indicating that quite likely the understory in these stands was quite a bit more open than in our study stands. This was expected,

as the management efforts (e.g., regular spacing, vigorous planting stock) were aimed at accelerating the development of tree cover.

A detailed analysis of the understory plant community indicated that the vegetation community composition in Philomath and Astoria were most strongly influenced by stand density (basal area) and age of all planted and natural regenerated tree species (Table 4). Additionally in Astoria, plant community composition was related to the presence of needle cover. However, needle cover was confounded by density, and other variables such as bare ground, rocks, or stumps, were not influential. Vegetation composition in Forest Grove was mainly influenced by elevation.

Shrubs

High overstory densities were indicative of lower shrub cover in Philomath and Astoria, but the influence of density on shrub cover decreased throughout time (Table 3). In both districts shrub cover was greater on higher quality sites and increased with age in Philomath. This increase is likely

Table 4.   Coefficients of correlation (R^2) of environmental and species variables with NMS ordination axes. Coefficients were reported if R^2 was $\geq$ 0.3. Bold numbers indicate an association with the axes. Vegetation community composition in Philomath was most strongly influenced by basal area (Axis 1, R^2 = 0.44) for example, and species such as *Pteridium aquilinum* had a negative association with Axis 1 therefore exhibiting greater abundance in low-density plots.

|	Association with axis	Axis 1	Axis 2	Axis 3
Philomath				
Environment matrix				
Basal area	+	**0.44**	0.00	0.00
Age	+	**0.34**	0.12	0.05
Elevation	+	0.00	**0.30**	0.01
Site prep-slash and burn	+	0.10	**0.41**	0.01
Species matrix				
Acer circinatum	+	0.02	**0.42**	0.05
Anaphalis margaritacea	−	**0.37**	0.00	0.00
Berberis nervosa	+	0.10	**0.52**	0.02
Dicentra formosa	+	0.04	0.02	**0.31**
Gaultheria shallon	−	0.18	0.03	**0.58**
Lotus crassifolius	−	**0.52**	0.00	0.00
Pteridium aquilinum	−	**0.46**	0.02	0.23
Rubus ursinus	−	**0.34**	0.13	0.02
Sambucus racemosa	+	0.07	0.03	**0.45**
Astoria				
Environment matrix				
Basal area	+	**0.70**	0.00	0.00
Age	+	**0.41**	0.00	0.00
Needle litter	+	**0.48**	0.02	0.02
Species matrix				
Anaphalis margaritacea	−	**0.30**	0.02	0.03
Berberis nervosa	−	0.00	0.01	**0.66**
Pteridium aquilinum	−	**0.33**	0.06	0.18
Rubus ursinus	−	**0.54**	0.00	0.03
Forest Grove				
Environment matrix				
Elevation	+	**0.54**	0.00	0.00
Species matrix				
Vaccinium parvifolium	+	**0.60**	0.00	0.00
Grass spp.	+	0.22	**0.34**	0.01
Lotus crassifolius	+	0.00	**0.42**	0.16
Pteridium aquilinum	+	0.10	0.01	**0.35**
Rubus ursinus	−	0.02	0.01	**0.30**

caused by a combination of shrub recovery after damage from harvesting or early release operations and of a shift in species composition. High overstory density stands in Forest Grove were correlated with low shrub cover with no recovery throughout time. Apparently, in Forest Grove the influence of the large range in elevation overshadowed the impact of stand density and may be responsible for the inconsistencies between the results from Forest Grove and the other two districts.

Forbs

Forb cover was lower on high-density plots in Philomath and Astoria, but showed no relation to density in Forest Grove (Table 3). In all three districts, forb cover did not show any trends with age. The different responses of understory vegetation is probably caused by a combination of the amount and composition of vegetation in the earlier preharvest stands, weed control practices, invasion potential (e.g., seed sources), and environmental and resource conditions as modified by tree regeneration. In addition, different site preparation techniques were used in each district and although not strikingly evident in the community analysis (Table 4; i.e., Philomath, $R^2=0.10$), could perhaps be another explanation for the inconsistencies.

Overall, species responded individually and differed in their abundances and ability to survive in the understory throughout the chronosequence. Although our study did not cover the first 4 years after the harvesting disturbance (Schoonmaker and McKee 1988) and included fairly homogenous conditions in young stands, our sites seemed to exhibit a range of developmental patterns. Using the approach and species lists developed by Halpern (1989) species were grouped based on their seral origin and life history (Figures 2 and 3). Group A (labeled I3 in Halpern 1989) contained *Agoseris* spp. and *Cirsium* spp., and were characterized as invader species that exhibited slow rates of occupancy throughout the study period. Group B (labeled I6 in Halpern 1989) contained other invaders (*Rubus parviflorus* and *Pteridium aquilinum*) that experienced a shift from increasing to decreasing occupancy. As shown in the community analysis, *Pteridium aquilinum* was most abundant in low-density areas (Table 4) but remained persistent in our oldest stands (Figure 2) by taking advantage of the variation (i.e., gaps) within stand. Generally, these invaders decreased in abundance in older stands (Figure 2; Table 4), but were not eliminated in these stands and remained in stands as late as age 20, the maximum age of our study sites.

We expected residual species (as defined by Halpern 1989) to show substantial reductions after the previous harvest. However, *Acer circinatum*, *Berberis nervosa*, *Corylus cornuta*, *Polystichum munitum* (group C, labeled R3 in Halpern 1989) were present, showed continuous recovery on our study sites (Figure 3), and even became dominant features in fairly young stands (>12 years). *Rubus ursinus* (group D, labeled R1 in Halpern 1989) was persis-

(a)

(b)
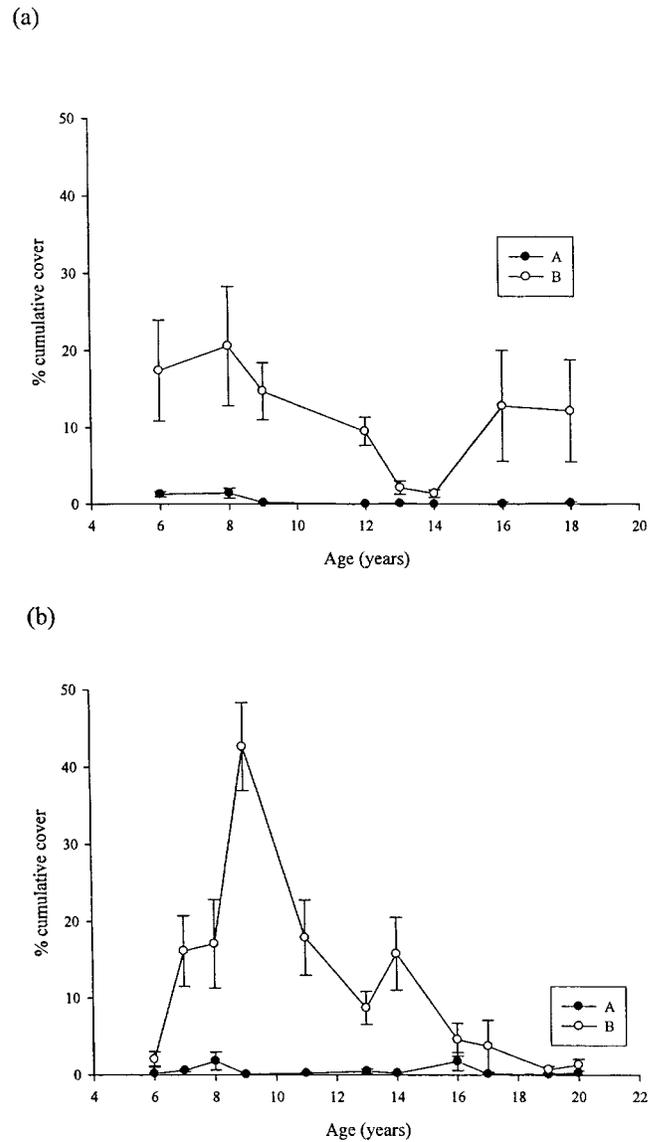
Figure 2. Cumulative percent cover (with SE bars) of group A (*Agoseris* spp., *Cirsium* spp.) and B (*Rubus parviflorus, Pteridium aquilinum*) invader species (as defined by Halpern 1989). Covers were summed for each plot and means calculated by age for Philomath (a) and Astoria (b).

tent in all cohorts but decreased in occupancy in the older stands.

Consequently, invader and residual species were all major contributors throughout the 20-year period. The dynamics of herbaceous and shrub layers were quite complex and in constant flux and general trends may not be associated with any successional stage (Halpern and Spies 1995) in these managed plantations. Instead, species vary in abundance and ability to survive throughout all stages depending on a combination of historical presence, disturbance timing and intensity, damage during harvesting and release operations, site preparation techniques, and resource availability (Schoonmaker and McKee 1988). Thus, the specific role of plantations in providing young successional habitat may have to be assessed on a case-by-case basis.

(a)
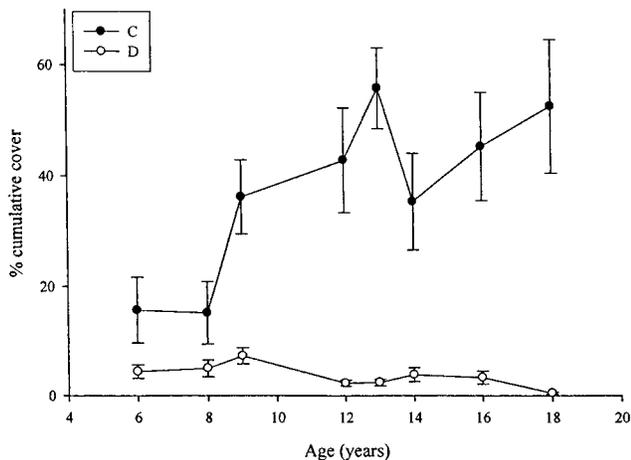
(b)

Figure 3. Cumulative percent cover (with SE bars) of group C (*Acer circinatum, Berberis nervosa, Corylus cornuta, Polystichum munitum*) and D (*Rubus ursinus*) residual species (as defined by Halpern 1989). Covers were summed for each plot and means calculated by age for Philomath (a) and Astoria (b).
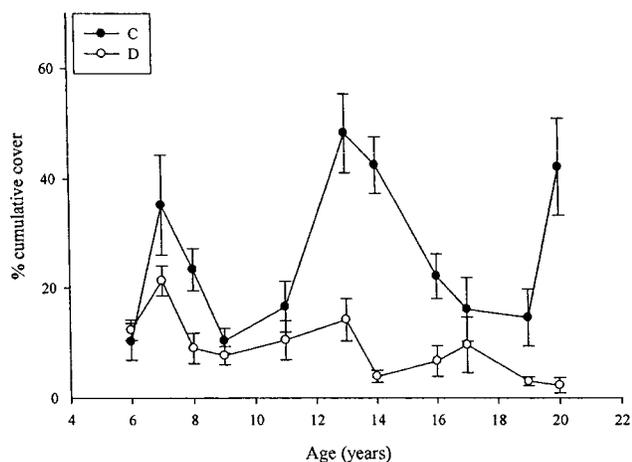
Conclusion

The study showed that stand development, as characterized by tree characteristics and understory vegetation, is influenced by density fairly early and is very dynamic in young plantations. It highlights that development of some critical stand structural components in managed plantations may not be captured well in many stand development classification schemes developed for natural stands (e.g., Bormann and Likens 1979, Carey and Curtis 1996, Oliver and Larson 1996, Spies and Franklin 1996). Although we did not measure changes in microclimate, the early shift in crown conditions and vegetation composition suggests functional changes in forest ecosystems. Thus, any gaps or openings in young plantations may provide opportunities for maintaining diversity of within stand conditions. In turn, this diversity may affect the role and impact of the stem exclusion phase. A study to investigate whether these openings can be maintained through management and used by wildlife species is currently underway.

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The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/*Pseudotsuga menziesii* stands

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Summary

1 We used repeated measurements of tree growth and population-level and neighbourhood conditions from three mixed *Alnus rubra*/*Pseudotsuga menziesii* forests in the Pacific Northwest, USA to investigate why previous results regarding the importance of neighbourhood competition as a determinant of plant growth were inconsistent.

2 We propose that relative dominance of a particular species determines the importance of neighbourhood interactions, and tested whether growth performance of both species at various stand ages agrees with this relative dominance hypothesis.

3 Neighbourhood and relative dominance interaction indices were modified to accommodate two-species mixtures and were incorporated into a growth model predicting relative diameter growth rates. The corrected Akaike Information Criterion (AIC_c) was used to identify the optimum interaction measures and model forms for each species and measurement period.

4 Interaction indices reflecting the size of a tree relative to the population were the best predictors of growth of the dominant (i.e. taller) species and neighbourhood interaction indices of the subordinate species.

5 Performance of interaction measures as predictors of relative growth rates in our study varied in agreement with the relative dominance hypothesis for both species and on all sites. Results from other studies suggest that the hypothesis may explain growth performances on a species and individual plant level and for a variety of life forms.

6 These findings suggest that the spatial scale of plant interactions is influenced by the size structure of plant populations. The relative dominance hypothesis offers a framework to provide insight into the mechanism of competition, based on the relative performance of competition indices.

Key-words: *Alnus rubra*, competition index, competitive asymmetry, neighbourhood competition, plant interaction, *Pseudotsuga menziesii*, relative dominance, relative growth rate, Akaike information criterion

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Introduction

The importance of plant–plant interactions in plant community structure and development has been well recognized (Yoda *et al.* 1963; Harper 1977; Tilman 1988; Duncan 1991; Peterson & Squiers 1995; Oliver & Larson 1996). These interactions may have positive effects on growth and survival through processes such as facilitation (for examples in forest ecosystems, see Binkley 1983;

Walker & Chapin 1987; Peterson & Squiers 1995) or negative effects through processes such as competition for resources (e.g. Ford 1975) and allelopathy (Williamson 1990). The predominant mode of interaction between trees in forest communities is, however, generally considered to be competition for resources (Oliver & Larson 1996). In many cases, early differences in size among trees due to variation in their emergence time (Connolly & Wayne 1996), their early growth rates (Turner & Rabinowitz 1983) and/or environmental heterogeneity (Hartgerink & Bazzaz 1984) are magnified as stands develop and competition for resources intensifies. In particular, inequalities in height within a population can result in the pre-emption of resources (e.g. light) by

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larger individuals, thus exacerbating the differences in growth rates among interacting trees (Cannell *et al.* 1984). Such competitive relationships, in which larger individuals obtain a disproportionate amount of available resources and suppress the growth of smaller individuals, have been referred to as size-asymmetric (Schwinning & Weiner 1998) and often lead to an increasingly positive correlation between the size of a tree relative to the population and its growth rate (Ford 1975; Cannell *et al.* 1984; Schmitt *et al.* 1987).

While size is often related to resource capturing capacity in populations in which competition is asymmetric (Ford & Diggle 1981; Miller & Werner 1987; Goldberg 1990; Schwinning & Weiner 1998), the amount of competition a tree experiences is also a function of the sizes and proximities of its neighbours (Mack & Harper 1977; Weiner 1982, 1984; Silander & Pacala 1985; Goldberg 1987). The influence of neighbourhood competition on plant growth has been well documented (e.g. Bella 1971; Weiner 1984; Penridge & Walker 1986; Peterson & Squiers 1995). However, our understanding of the relationship between this concept (referred to hereafter as the importance of competition *sensu* Weldon & Slauson 1986) and a plant's size relative to the population is limited. For example, several authors examining competition in populations with varied size structures have noted that measures of neighbourhood competition have only been able to explain the variation in growth of the smaller individuals in the population (e.g. Cannell *et al.* 1984; Kubota & Hara 1995; McLellan *et al.* 1997). In these studies, the effects of neighbourhood competition on larger individuals have been minimal, suggesting that the importance of neighbourhood competition as a determinant of tree growth may vary according to an individual's relative size. While neighbourhood measures incorporating the effects of size-asymmetrical competition have been developed to account for this variation (e.g. Penridge & Walker 1986; Thomas & Weiner 1989; Tomé & Burkhart 1989; Schwinning & Weiner 1998; Purves & Law 2002), these measures have assumed that neighbourhood competition is equally important for all individuals in a population irrespective of their size (Thomas & Weiner 1989).

The influence of plant size is further complicated. In populations in which competition is asymmetric, large individuals often obtain a disproportionate share of resources and suppress the growth of smaller individuals (e.g. Connolly & Wayne 1996). Under these conditions, the amount of resources available to smaller individuals within the population is strongly related to the amount of neighbourhood competition from larger neighbours only (Thomas & Weiner 1989; Schwinning & Weiner 1998). Although the amount of resources available to dominant individuals may also be affected by neighbourhood competition, only weak relationships have been observed in several studies between measures of neighbourhood competition and the growth of larger individuals (Cannell *et al.* 1984) or taller species (Kubota & Hara 1995; McLellan *et al.* 1997;

Wagner & Radosevich 1998). This suggests that the superior resource capturing capacity of a dominant plant may be a more important determinant of its growth than neighbourhood competition (Wagner & Radosevich 1998). The changes to population and neighbourhood conditions that result from differences in long-term growth rates among interacting individuals and stochastic events could also lead to changes in the importance of neighbourhood competition over time (e.g. Daniels *et al.* 1986; Stoll *et al.* 1994). We propose the 'relative dominance hypothesis', which states that changes in the relative dominance of a particular species may result in changes in the importance of neighbourhood interactions over time. Repeated measurements of tree growth and population-level and neighbourhood conditions from three mixed *Alnus rubra* Bong./*Pseudotsuga menziesii* [Mirb.] Franco (nomenclature follows Hitchcock & Cronquist 1976) forests in the Pacific Northwest, USA are used to test this hypothesis.

Methods

STUDY SPECIES AND SITES

Alnus rubra and *Pseudotsuga menziesii* commonly co-occur throughout the Pacific Northwest and the interactions between these two species at different stages of forest development have received a great deal of attention (e.g. Puettmann *et al.* 1992; Shainsky & Radosevich 1992). Mixed forests of these two species provide an excellent test system for examining the relative dominance hypothesis due to the differences in their growth rates and resource requirements. *A. rubra* is a fast-growing, early successional species that is often able to attain its mature height within 40 years (Newton & Cole 1994). Its ability to fix nitrogen also provides an opportunity to investigate positive (i.e. facilitation) as well as negative (i.e. competition) interactions (Binkley 1983). In contrast, *P. menziesii* is a long-lived, early to late-successional species and, although intial growth rates are less than *A. rubra*, it is able to maintain height growth for up to two hundred years (Curtis *et al.* 1974). The mixed *Alnus rubra*/*Pseudotsuga menziesii* stands studied consisted of two established replacement series studies at the Cascade Head and H.J. Andrews Experimental Forests in western Oregon, USA, and a natural stand at Delezene Creek in western Washington, USA (see Table 1 for locations and climatic and soil properties).

EXPERIMENTAL DESIGN

The experimental design of the Cascade Head (CH) and H.J. Andrews (HJA) study sites is a replacement series (de Wit 1960; Jolliffe 2000) consisting of six proportions (0 : 100, 10 : 90, 30 : 70, 50 : 50, 75 : 25, and 100 : 0%) of *A. rubra* and *P. menziesii* replicated three times at each site in a randomised, complete block design (Fuentes-Rodríquez 1994). These sites were prepared for planting by clearcutting and slash burning in 1984

Table 1 Locations and climatic and site characteristics of the study areas

Study site/location	Lat. N, Long. W	Soil drainage class/texture	Soil parent material	Elevation (m)	Mean minimum temperature (°C)	Mean maximum temperature (°C)	Precipitation (cm)
Cascade Head Experimental Forest, Oregon, USA	45°05′ N, 124°00′ W	Well-drained, fine loams*	Basalt	150–330	2.2	20.9	250
H.J. Andrews Experimental Forest, Oregon, USA	44°14′ N, 122°10′ W	Well-drained, coarse loams†	Andesite	500–800	−8.5	26.9	230§
Delezene Creek, Oakville, Washington, USA	46°56′ N, 123°24′ W	Well-drained, fine loams‡	Sandstone	60–130	1	21.5	250¶

*Shipman (1997).
†Patching (1987).
‡Pringle (1986).
§Halpern (1989).
¶WRCC (2001).

and were planted in 1986 with 2-year old *A. rubra* and 1-year old *P. menziesii* seedlings on a 3 × 3 m, grid. Each plot consisted of 9 rows with 9 seedlings and species were intermixed (Fuentes-Rodríquez 1994). Three additional replicates of the replacement series were established at each site with *P. menziesii* planted in 1986, but *A. rubra* planting delayed until the fifth year. It is important to note that, despite the initial grid-based spacing, random mortality and variation in seedling placement, as well as the differences in timing of alder plantings, created a range of spatial and size conditions in these plots.

The stand at Delezene Creek (DC) is a naturally regenerated, even-aged mixture of *A. rubra* and *P. menziesii* that was inventoried repeatedly from 1952 to 1978 by students from University of Washington and again in 1990 by D.E. Hibbs and K.J. Puettmann. A complete stem map of the 1-ha study area was created in 1959. At the time of initial measurement (1952), the stand was 30 years old. Other tree species were present at all three study sites, including *Tsuga heterophylla* and *Picea sitchensis*. However, these species occurred at very low frequencies and were only found as understorey seedlings or saplings.

FIELD SAMPLING

On the replacement series sites, trees were measured in 15 × 15 m plots in the centre of each replicate (the outer two rows were left as unmeasured buffers), with the CH and HJA sites contributing 33 and 30 plots, respectively. Species, diameter at breast height (D), total tree height, height to base of live crown and crown diameter (average of 2 perpendicular crown diameter measurements) were recorded for each tree in 1991, 1992, 1993, 1995, 1998 and 2001. The stands were 15 years old at the time of last measurement. Locations of trees were mapped in the summer of 2001 and converted to metric coordinates. For multiple stemmed individuals, stump location and breast height location of each stem were recorded and a single value of diameter at breast height was calculated by summing the basal areas at breast height of each stem and deriving the D represented by the total basal area.

For the DC site, species and D were recorded for each tree in 1952, 1957, 1961, 1965, 1969, 1975, 1978 and 1990. At each date, height measurements were taken from a subset of trees representative of the range of tree sizes for *P. menziesii* and *A. rubra* in the stand. We estimated missing heights using ratio estimation (Som 1996). The stand was harvested after the final measurement in 1990.

INTERACTION INDICES

Intra- and inter–specific interaction indices, designed to represent various aspects of the nature and degree of interaction between trees, were calculated for each tree at each site and measurement period. The set of indices listed in Table 2 was selected based on their successful performance in previous studies examining competitive interactions in forest stands (e.g. Biging & Dobbertin 1992; Richardson *et al*. 1999) and to represent a range of complexity (e.g. distance independent and dependent, relative diameter or crown sizes of neighbouring trees). These indices were modified to accommodate two-species mixtures allowing for separation of intra- and inter–specific interactions on individual tree growth.

Interaction indices (IIs) selected were categorized into two broad classes (Table 2). Neighbourhood (N) interaction indices (referred to as 'proximity indices' in the recent review by Weigelt & Jolliffe 2003) were calculated from various characteristics of neighbouring trees and were used to characterize the influence of neighbourhood interactions on the resources available for tree growth (**B**, **BE**, **H**, **L**, and **R** in Table 2). Neighbouring trees were defined as trees within a radius centred on the focal tree except for the **BE** index, where a circular area of influence (A_i) was constructed for all trees using crown diameter measurements. In contrast to the other neighbourhood interaction indices, **BE** defined the influence of a neighbouring tree on the resources available to a focal tree as a function of the degree of overlap between its area of influence and that of the focal tree. In addition, the ratio of diameters between neighbouring trees was also utilized in the **BE** index to represent size–symmetrical interactions. Bella (1971) incorporated a scaling exponent into this term to express

Table 2 Neighbourhood (N) and relative dominance (RD) interaction indices used to characterize tree–tree interactions. All interaction indices have been modified to separate intra- and inter–specific interactions

Source	Symbol	Interaction Index (II)	Type
Biging & Dobbertin (1992)	**B**	$B_{i1} = \left[\sum_{j_1=1}^{n_1} \left(\frac{V_{j1}/V_{i1}}{L_{i1j1}} \right) \right] + \left[\sum_{j_2=1}^{n_2} \left(\frac{V_{j2}/V_{i1}}{L_{i1j2}} \right) \right]$	N
Bella (1971)	**BE**	$BE_{i1} = \left[\sum_{j_1=1}^{n_1} \left(\frac{O_{i1j1}}{A_{i1}} \right) \left(\frac{D_{j1}}{D_{i1}} \right)^b \right] + \left[\sum_{j_2=1}^{n_2} \left(\frac{O_{i1j2}}{A_{i1}} \right) \left(\frac{D_{j2}}{D_{i1}} \right)^b \right]$	N
Glover & Hool (1979)	**G**	$G_{i1} = \left[\left(\frac{B_{i1}}{\bar{B}_1} \right) + \left(\frac{B_{i1}}{\bar{B}_2} \right) \right] \Big/ 2$	RD
Hegyi (1974)	**H**	$H_{i1} = \left[\sum_{j_1=1}^{n_1} \left(\frac{D_{j1}/D_{i1}}{L_{i1j1}} \right) \right] + \left[\sum_{j_2=1}^{n_2} \left(\frac{D_{j2}/D_{i1}}{L_{i1j2}} \right) \right]$	N
Lorimer (1983)	**L**	$L_{i1} = \left[\sum_{j_1=1}^{n_1} \left(\frac{D_{j1}}{D_{i1}} \right) \right] + \left[\sum_{j_2=1}^{n_2} \left(\frac{D_{j2}}{D_{i1}} \right) \right]$	N
Richardson *et al.* (1999)	**R**	$R_{i1} = \left[\frac{1}{H_{i1}^2} \frac{1}{n_1} \sum_{j_1=1}^{n_1} (H_{j1})^2 (Af_{j1}) \right] + \left[\frac{1}{H_{i1}^2} \frac{1}{n_2} \sum_{j_2=1}^{n_2} (H_{j2})^2 (Af_{j2}) \right]$	N
Wykoff *et al.* (1982)	**W**	$W_{i1} = \left[\sum_{\substack{j_1=1 \\ D_j > D_i}}^{p_1} (D_{j1})^2 0.00007854 \right] + \left[\sum_{\substack{j_2=1 \\ D_j > D_i}}^{p_2} (D_{j2})^2 0.00007854 \right]$	RD

A_i = area of influence of focal tree i.
Af_j = arc fraction of neighbour j's crown, defined as: $Af_j = \{2 \times \tan^{-1}(R_j/L_{ij})/360\}$.
L_{ij} = distance between neighbour j and focal tree i.
R_j = crown radius of neighbour j.
b = scaling exponent (1.0, 1.5, 2.0).
$\bar{B}$ = basal area of tree with mean D within a stand.
B_i = basal area of focal tree i.
D_i = diameter at breast height of focal tree i.
D_j = diameter at breast height of neighbour tree j.
H_i = height of focal tree i.
H_j = height of neighbour tree j.
n = total number of neighbours.
O_{ij} = area of influence overlap between focal tree i and neighbour j.
p = total number of trees in the population.
V_i = crown volume of focal tree i.
V_j = crown volume of neighbour tree j.
1, 2 = species.

the degree to which resources were shared disproportionately, i.e. size-asymmetrically (*sensu* Schwinning & Weiner 1998). Based on findings of past research (e.g. Bella 1971; Holmes & Reed 1991; Biging & Dobbertin 1992), we used **BE** indices with scaling exponents set at 1, 1.5, and 2.

Relative dominance (RD) interaction indices were computed from characteristics of all trees within a given stand, rather than just those of neighbours. As a result, they serve as an expression of the size of an individual tree relative to the overall population. Glover & Hool's (1979) index (**G** in Table 2) uses the ratio of the basal area of the focal tree relative to that of a tree whose D has the same value as the mean for the population. This index assumes that the interactions experienced by a focal tree are strictly a function of its relative size (i.e. perfect size symmetry *sensu* Schwinning & Weiner 1998) and does not therefore incorporate a measure of density. A second relative dominance index, **W**, developed

by Wykoff *et al.* (1982) assumes that the focal tree interacts only with trees in the population that are larger than it. In contrast to **G**, this index also includes a measure of density (of larger individuals), as basal areas of all trees larger (in basal area) than the focal tree were summed.

Measurements taken at CH and HJA sites allowed calculation of all the various indices, but only indices using D (to characterize tree size) and intertree distances could be calculated at DC (**G**, **H**, **L**, and **W** in Table 2). Only single stemmed trees were used as focal individuals in calculation of the interaction indices, but multiple stemmed individuals were considered as neighbours. To avoid plot edge biases, only trees occurring at least 3 m from the measurement plot border at the CH and HJA sites and at least 9 m from the study site border at the DC site were selected as focal trees. However, all trees within the study sites were considered as neighbours in calculating the interaction indices.

A set of search radii was used to determine neighbouring trees (with the exception of **BE**, which utilized the area of overlap). For the CH and HJA sites, the maximum radii were restricted to 4.5 m to make use of as many trees as possible while avoiding neighbourhoods that extended beyond the plot borders. We used the central tree in each plot, for which we could calculate the largest neighbourhood, to investigate whether this was a restrictive assumption and compared results of analyses using search radii of 3.0, 4.5, and 6.0 m. Search radii of 3.0, 4.5, 6.0, 7.5, 9.0, and 11.5 m were used in the calculation of the neighbourhood indices for the DC study site.

ANALYSIS

The relative diameter growth rate (*RGR*) was selected as a measure of performance (i.e. of the response to interactions experienced by the focal tree). *RGR* was calculated for each measurement period as:

$$RGR = \frac{\ln D_2 - \ln D_1}{t_2 - t_1} \qquad \text{eqn 1}$$

where D_1 and D_2 are the diameters at the beginning (t_1) and end (t_2) of the measurement period. This measure accounts for initial size at the beginning of a measurement period, thus allowing for a more accurate assessment of the relative importance and intensity of tree–tree interactions at different stages of stand development (Ford & Sorrensen 1992).

A growth model, which incorporated intra- and inter–specific interactions, was developed to evaluate the intensity and importance of tree–tree interactions over each measurement period. The main growth model used was:

$$RGR_i = \beta_0 + \beta_1 \cdot \ln(II_{11}) + \beta_2 \cdot \ln(II_{12})$$
$$+ \beta_3 \cdot \ln(II_{11} \cdot II_{12}) + \varepsilon \qquad \text{eqn 2}$$

where II_{11} and II_{12} are the intra- and inter–specific interaction indices (without units) at the beginning of the growth interval, $II_{11} \cdot II_{12}$ is the statistical interaction between intra- and inter–specific interaction indices, and ε is the error term. In addition to the full model (Equation 2), models only incorporating intra or inter–specific interactions were evaluated for each growth interval and interaction index using mixed linear regression analyses performed in SAS (PROC MIXED; SAS Institute 1999). It is important to note that the choice of growth models using these interaction indices is determined by the study conditions. For example, Richardson *et al.* (1999) used an exponential growth model as their data were limited to very young seedlings, which have been shown to exhibit exponential growth. Consequently, the absolute results of comparisons in any study cannot be directly compared with results of other studies. Instead, any comparison of different studies should be limited to relative performances, and this assumes proper choice of models in all studies as evidenced by residual analysis. With one exception (**W**

interaction index for *P. menziesii* years 6–9 at HJA), non-linearity and non-homogeneous variance was corrected by logarithmic transformation of independent variables in the growth models. Spatial correlation between trees in each plot was accounted for by including a power spatial correlation structure in each of the models (SP(POW); SAS Institute, Inc. 1999). This structure accounts for the covariance between trees due to spatial location based on the *x*-y coordinates of each tree. For the CH and HJA study sites, random plot effects were also incorporated into the models to account for variation in growing conditions across plots.

For each measurement period, a set of models containing all possible interaction indices was constructed. The corrected Akaike Information Criterion, AIC_c, was used to determine the best index and neighbourhood size for each measurement period and to test the relative fit of each model (Burnham & Anderson 1998). AIC_c is derived from the maximum log-likelihood estimate and number of parameters in a given model, rewarding models for goodness of fit and imposing penalties for multiple parameters. Smaller AIC_c values indicate better models and AIC_c values are ranked according to the difference between the AIC_c value for a given model (AIC_{ci}) and the lowest AIC_c value in a given set of models (AIC_{cmin}): $\Delta_i = AIC_{ci} - AIC_{cmin}$. The difference value, Δ_i, allows a strength of evidence comparison among the models, where increasing Δ_i values correspond with decreasing probability of the fitted model being the best approximating model in the set (Anderson *et al.* 2000). As a rule of thumb, models with $\Delta_i \le 2$ have considerable support and should be considered when making inferences about the data (Burnham & Anderson 2001).

To approximate the probability of a model being the best in a given set, the Δ_i values were used to calculate Akaike weights (w_i) using the following formula (Burnham & Anderson 1998):

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^{R} \exp(-\Delta_{ir}/2)} \qquad \text{eqn 3}$$

where w_i is the Akaike weight for model *i* and *R* is the number of models in the set. Although performances are only reported in this paper for well supported models (i.e. $\Delta_i \le 2$), w_i values calculated using all Δ_i values provide an approximation of how other models in the set performed relative to the best selected models.

A null model was included in each set of candidate models to determine the importance of interactions on relative growth rates over the measurement period. The null model stated that the relative growth rate over a given measurement period was solely a function of the spatial correlation among trees in a given population and the model did not therefore include any terms describing tree–tree interactions. Models incorporating measures of interaction that had lower Δ_i values than the null model indicated situations where tree–tree interactions were more important than other unmeasured factors,

such as genetic variation and environmental heterogeneity, which also affect relative diameter growth rates (Weldon & Slauson 1986).

In cases in which the best models for the CH and HJA sites contained neighbourhood interaction indices, the appropriate neighbourhood size was determined by fitting models for the central tree in each plot using neighbourhood radii of 3.0, 4.5 and 6.0 m and comparing the Δ_i values. If the models using 3.0 and/or 4.5 m radii were ranked higher than the models with larger neighbourhoods (i.e. 6.0 m) it was assumed that the neighbourhood sizes used in our analyses were appropriate for the site and species.

Results

The density, height, and diameter of *A. rubra* and *P. menziesii* in the young (CH and HJA) and mature (DC) stands for all measurements are shown in Figure 1. On average, *A. rubra* in the young stands had larger heights

than *P. menziesii*, whereas *P. menziesii* was taller in the mature stand (Fig. 1). Diameter at breast height followed a similar pattern (Fig. 1). Very little mortality occurred in the young stands (Fig. 1), but roughly 30% of the *A. rubra* and 22% of the *P. menziesii* in the mature stand died between ages 30–68 (sample sizes for D in Fig. 1c).

ANALYSIS OF TREE–TREE INTERACTIONS

The null models for both species and in all measurement periods had Δ_i values greater than 2.0 indicating that tree–tree interactions and the other measured factors were important to the relative growth rates of *A. rubra* and *P. menziesii* in both young and mature stands.

Specific spatial information, i.e. neighbour tree distances, did not improve our ability to characterize the nature of interaction in these stands. With few exceptions, models employing a neighbourhood interaction index that did not weight neighbour tree influence by proximity (**L**, **BE** in Table 2) and/or models containing
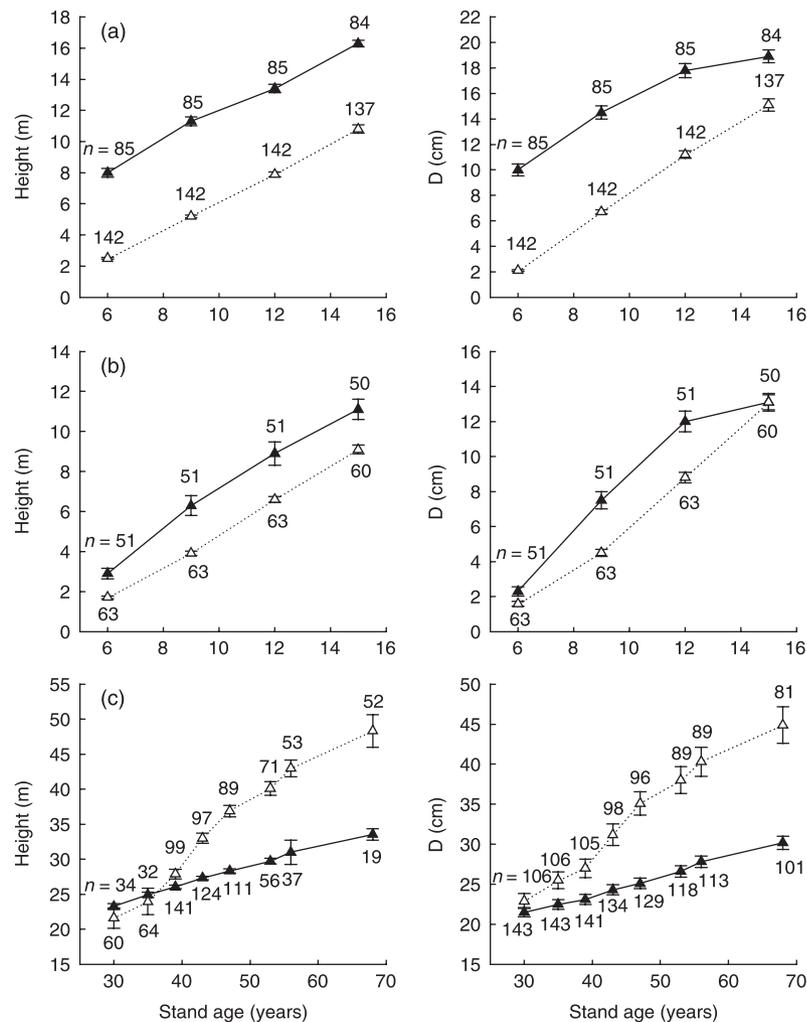
Fig. 1 Mean height and diameter at breast height (D) of *Alnus rubra* (▲) and *Pseudotsuga menziesii* (△) over time at the (a) Cascade Head (CH), (b) H.J. Andrews (HJA), and (c) Delezene Creek (DC) study sites. Error bars represent standard errors and *n* gives the number of observations in a sample (Note: height was only measured on a subset of trees representing a range of tree sizes at the DC study site).

Table 3 AIC_c model comparisons of selected models (i.e. $\Delta_i \leq 2.00$) for quantifying the effects of intra- and inter–specific interactions on *Pseudotsuga menziesii* relative growth rates over the measurement periods examined (years 6–9, 9–12, and 12–15) in the young stands (CH and HJA)

Site	Y^a	II^b	Radius	Model[c]	K^d	AIC_c^e	Δ_i^f	w_i^g
CH	6–9	**G**	–	Intra-specific	5	−317.9	0.00	0.67
		G	–	Intra-specific, interspecific, intra × interspecific	7	−316.5	1.44	0.32
	9–12	**BE 1***	A_i^{γ}	Inter-specific	5	−505.5	0.00	0.24
		BE 1.5	A_i	Inter-specific	5	−504.6	0.93	0.16
	12–15	**R**	4.5	Intra-specific	5	−537.5	0.00	0.17
		B	4.5	Inter-specific	5	−536.1	1.39	0.09
HJA	6–9	**G**	–	Intra-specific, interspecific, intra × interspecific	7	−99.4	0.00	0.98
	9–12	**L**	3.0	Intra-specific, interspecific, intra × interspecific	7	−213.5	0.00	0.25
		L	4.5	Intra-specific, interspecific, intra × interspecific	7	−213.1	0.34	0.21
	12–15	**BE 2**	A_i	Intra-specific, interspecific, intra × interspecific	7	−329.7	0.00	0.17
		BE 1.5	A_i	Intra-specific, interspecific, intra × interspecific	7	−329.5	0.24	0.15
		BE 1	A_i	Intra-specific, interspecific, intra × interspecific	7	−329.2	0.55	0.13
		B	4.5	Intra-specific	5	−329.1	0.63	0.13
		B	3.0	Intra-specific	5	−328.9	0.80	0.12
		B	4.5	Intra-specific	5	−328.8	0.89	0.11
		L	4.5	Intra-specific, interspecific, intra × interspecific	7	−328.5	1.19	0.10
		B	3.0	Intra-specific, interspecific, intra × interspecific	7	−327.7	1.99	0.06

*Scaling exponent (1.0, 1.5, 2.0).
[γ]Area of influence of focal tree.
[a]Measurement period.
[b]Interaction index (*II*) used to measure intra- and inter–specific interactions (see Table 2).
[c]Parameters included in growth model.
[d]Total number of model parameters including the intercept, variance, and covariance parameters.
[e]Corrected Akaike Information Criterion.
[f]Difference between model AIC_c value and minimum AIC_c value.
[g]Probability of model being the best in a given set.

a relative dominance interaction index (**G** and **W**) were more likely to be the best model in the set (i.e. $\Delta_i < 2$) than those weighting neighbour influence by distance (**B**, **H**, and **R** in Table 2). We found no differences in the ranking of interaction indices selected for predicting relative growth rates when the power spatial correlation structure was removed (data not shown), suggesting that these results are not a consequence of accounting for spatial correlation in these models.

In the young stands, several of the best models for both species contained the neighbourhood interaction index (**BE**) that used the area of influence (A_i) (Tables 3 and 4). Weighting of **BE** for size–asymmetrical interactions was unnecessary as there was no distinguishable difference between the fit of models with the three different

scaling exponents, indicating perfect size-symmetry (*sensu* Schwinning & Weiner 1998). Evaluations of appropriate neighbourhood sizes using the central trees in CH and HJA plots indicated that neighbourhoods with a 3.0 m and 4.5 m radius were appropriate in these young stands (Table 5). However, these results should be interpreted cautiously due to the small sample size. The range of neighbourhood sizes used in the mature stand was also appropriate, as all neighbourhood interaction indices included in the set of best models had neighbourhood sizes less than the maximum neighbourhood size employed (≤ 11.5 m) (Tables 6 and 7).

It is interesting to note that there was strong evidence, for both species, that effects of inter–specific interactions were not exclusively additive to effects of intra–specific

Table 4 AIC_c model comparisons of selected models for quantifying the effects of intra- and inter–specific interactions on *Alnus rubra* relative growth rates over the measurement periods examined (years 6–9, 9–12, and 12–15) in the young stands (CH and HJA). For definitions of symbols see Table 3

Site	Y	II	Radius	Model	K	AIC_c	Δ_i	w_i
CH	6–9	**W**	–	Intra-specific	5	−316.7	0.00	0.33
		W	–	Inter-specific	7	−315.8	0.88	0.21
	9–12	**G**	–	Intra-specific, interspecific, intra × interspecific	7	−360.4	0.00	0.68
	12–15	**L**	3.0	Inter-specific	5	−256.5	0.00	0.24
		L	4.5	Inter-specific	5	−256.1	0.34	0.21
		BE 2.0	A_i	Inter-specific	5	−255.4	1.10	0.14
HJA	6–9	**G**	–	Intra-specific, interspecific, intra × interspecific	7	−94.4	0.00	0.63
		G	–	Intra-specific	5	−93.3	1.09	0.36
	9–12	**G**	–	Intra-specific	5	−144.0	0.00	0.44
	12–15	**L**	3.0	Intra-specific, interspecific, intra × interspecific	7	−105.6	0.00	0.18
		L	4.5	Intra-specific, interspecific, intra × interspecific	7	−105.1	0.50	0.14

Table 5 Evaluations of appropriate neighbourhood sizes for *Pseudotsuga menziesii* and *Alnus rubra* occurring in the plot centres at the CH and HJA sites. For definitions of symbols see Table 3

Species	Site	Y	n^h	II	Radius	K	AIC_c	Δ_i	w_i
Pseudotsuga menziesii	CH	12–15	13	**R**	4.5	5	−20.2	0.00	0.33
			13	**R**	3.0	5	−19.4	0.83	0.21
			13	**R**	6.0	5	−19.3	0.97	0.19
			13	**B**	4.5	5	−18.1	2.16	0.10
			13	**B**	3.0	5	−18.0	2.23	0.10
			13	**B**	6.0	5	−17.5	2.69	0.07
	HJA	9–12	12	**L**	4.5	5	−10.6	0.00	0.65
			12	**L**	3.0	5	−8.1	2.49	0.18
			12	**L**	6.0	5	−8.0	2.65	0.17
	HJA	12–15	10	**B**	3.0	5	−3.6	0.00	0.27
			10	**B**	4.5	5	−3.6	0.00	0.27
			10	**B**	6.0	5	−3.0	0.61	0.14
			10	**L**	3.0	5	−2.6	1.03	0.14
			10	**L**	4.5	5	−2.6	1.03	0.15
			10	**L**	6.0	5	2.6	6.18	0.03
Alnus rubra	CH	12–15	14	**L**	3.0	5	−21.3	0.00	0.60
			14	**L**	4.5	5	−20.1	1.20	0.33
			14	**L**	6.0	5	−16.6	4.68	0.07
	HJA	12–15	13	**L**	4.5	5	−8.2	0.00	0.38
			13	**L**	3.0	5	−8.0	0.18	0.36
			13	**L**	6.0	5	−7.6	0.60	0.26

[h]Number of centre trees used in regression.

interactions. Not only did the best models contain the interaction terms (Tables 3, 4, 6, and 7) but, in several cases in the young stands, parameters for intra–specific interactions had a positive sign when predicting on *P. menziesii* relative growth rates (e.g. years 12–15 at CH, Table 3, Intra–specific interaction parameter = 0.018 ± 0.012). These positive parameter estimates may be a function of multicollinearity, i.e. the interactions from *P. menziesii* are less negative relative to interactions from *A. rubra* in the young stands.

INTERACTION DYNAMICS

Alnus rubra

The importance of neighbourhood interactions compared to that of size relative to the population as predictors of relative growth rates varied between the young and mature stands. In general, size relative to the population was a better predictor of *A. rubra* relative growth rates in young stands, as the majority of best

Table 6 AIC_c model comparisons of selected models for quantifying the effects of intra- and inter–specific interactions on *Pseudotsuga menziesii* relative growth rates over the measurement periods (years 30–35, 35–39, 39–43, 43–47, 47–53, 53–56, and 56–68) examined in the mature stand (DC). For definitions of symbols see Table 3

Y	II	Radius	Model	K	AIC_c	Δ_i	w_i
30–35	**H**	4.5	Intra-specific, interspecific, intra × interspecific	6	−1076.8	0.00	0.30
	G	–	Intra-specific, interspecific, intra × interspecific	6	−1076.7	0.11	0.29
	H	3.0	Intra-specific, interspecific, intra × interspecific	6	−1075.8	1.00	0.18
35–39	**H**	9.0	Intra-specific	4	−777.5	0.00	0.54
39–43	**L**	9.0	Intra-specific	4	−593.2	0.00	0.26
	H	9.0	Intra-specific, interspecific, intra × interspecific	6	−593.0	0.20	0.23
	H	7.5	Intra-specific, interspecific, intra × interspecific	6	−591.6	1.57	0.12
43–47	**G**	–	Intra-specific, interspecific, intra × interspecific	6	−560.0	0.00	0.64
47–53	**W**	–	Inter-specific	4	−583.8	0.00	0.40
	W	–	Intra-specific, interspecific, intra × interspecific	6	−583.4	0.41	0.32
	G	–	Intra-specific, interspecific, intra × interspecific	6	−583.1	0.64	0.29
53–56	**W**	–	Inter-specific	4	−560.1	0.00	0.46
56–68	**W**	–	Inter-specific	4	−550.7	0.00	0.70

models used relative dominance interaction indices (Table 4). It is important to note that the high performance of the relative dominance interaction index **W** over the earliest measurement period (years 6–9) at the CH site suggests that population density was also influencing *A. rubra* relative growth rates, whereas the selection of the relative dominance interaction index **G** over the same period at the HJA site suggests that only size determined growth rates here (Table 4). The positive inter–specific interaction effects on *A. rubra* relative growth rates over years 12–15 at the CH site (e.g. Tables 4, **L** with 3.0 m radius, Inter–specific interaction parameter = 0.037 ± 0.021) and the negative intra- and inter–specific interactions over the same period at the HJA site (e.g. Tables 4, **L** with 3.0 m radius, Intra–specific interaction parameter = −0.017 ± 0.021 and Inter–specific interaction parameter = −0.087 ± 0.015) indicate increased intensity of neighbourhood interactions from other large *A. rubra* at the CH site and from codominants of both species at HJA. These increases coincide with the shift in the nature of interactions from the population to the neighbourhood-level (Table 4).

There was strong evidence that neighbourhood interactions were more important to *A. rubra* relative growth rates in the mature stand as all the best models used neighbourhood interaction indices (Table 7).

Similar to the young stands, the importance of neighbourhood interactions in the mature stand was expressed during the periods *A. rubra* occupied codominant and subordinate canopy positions (Fig. 1c).

Pseudotsuga menziesii

In general, neighbourhood interactions were also important for *P. menziesii* relative growth rates in young stands (the majority of best models used neighbourhood interaction indices, Table 3). However, over the earliest measurement period examined (years 6–9) the index using size relative to the population was more important than neighbourhood or population–level interactions (the best models contained the interaction index, **G**, Table 3). In the mature stand, the importance of size relative to the population compared to neighbourhood interactions changed as *P. menziesii* attained a dominant canopy position. During periods where heights of the two species were similar (years 30–43, Fig. 1c), neighbourhood interactions were a better predictor of *P. menziesii* relative growth rates (Table 6). However, once *P. menziesii* had attained a dominant canopy position (years 43–68, Fig. 1c), size relative to the population became a better predictor of relative growth rates, with all of the best models using relative dominance interaction indices (Table 6).

Table 7 AIC$_c$ model comparisons of selected models for quantifying the effects of intra- and inter–specific interactions on *Alnus rubra* relative growth rates over the measurement periods (years 30–35, 35–39, 39–43, 43–47, 47–53, 53–56, and 56–68) examined in the mature stand (DC). For definitions of symbols see Table 3

Y	II	Radius	Model	K	AIC$_c$	Δ_i	w_i
30–35	L	4.5	Intra-specific	4	−1321.6	0.00	0.17
	L	7.5	Intra-specific	4	−1321.6	0.05	0.17
	L	3.0	Intra-specific	4	−1321.6	0.05	0.17
	L	6.0	Intra-specific	4	−1321.5	0.14	0.16
	L	7.5	Intra-specific, interspecific, intra × interspecific	6	−1320.0	1.65	0.08
35–39	L	6.0	Intra-specific, interspecific, intra × interspecific	6	−1107.5	0.00	0.72
39–43	L	3.0	Intra-specific	4	−1001.0	0.00	0.16
	L	6.0	Intra-specific	4	−1000.4	0.56	0.12
	L	9.0	Intra-specific	4	−1000.2	0.76	0.11
	L	7.5	Intra-specific	4	−1000.0	0.97	0.10
	L	9.0	Intra-specific	4	−999.9	1.10	0.09
	L	7.5	Intra-specific, interspecific, intra × interspecific	6	−999.6	1.38	0.08
43–47	L	4.5	Intra-specific, interspecific, intra × interspecific	6	−981.7	0.00	0.29
	L	6.0	Intra-specific, interspecific, intra × interspecific	6	−980.7	0.99	0.18
	L	4.5	Intra-specific	4	−979.7	1.94	0.11
47–53	L	6.0	Intra-specific	4	−927.1	0.00	0.17
	L	4.5	Intra-specific	4	−926.7	0.38	0.14
	L	7.5	Intra-specific	4	−925.4	1.71	0.07
53–56	L	7.5	Inter-specific	4	−886.3	0.00	0.12
	L	6.0	Inter-specific	4	−885.5	0.82	0.08
	L	4.5	Inter-specific	4	−885.1	1.24	0.06
	L	3.0	Intra-specific	4	−884.5	1.80	0.05
	L	9.0	Inter-specific	4	−884.3	1.99	0.04
56–68	L	11.5	Inter-specific	4	−541.7	0.00	0.29
	L	11.5	Intra-specific, interspecific, intra × interspecific	6	−541.4	0.33	0.25

NEIGHBOURHOOD SIZE

The optimal extent of neighbourhoods for prediction of focal tree growth increased over time (stand age and/or tree size) for both species (Tables 3, 4, 6, and 7). For example, neighbourhood size resulting in best models for *P. menziesii* in the mature stand at age 30 was roughly 4.5 m (Table 6), increasing to 9.0 m at age 35 and over (Table 6). In general, in the mature stand good models for predicting *A. rubra* relative growth rates over the earlier years (30–43) included neighbourhood interaction indices with radii ranging from 3.0 to 9.0 m (Table 7) but, by age 56 and over the neighbourhood size had increased to 11.5 m for all such models (Table 7). However, during some measurement periods, the fits of models using different neighbourhood sizes were very similar, such as for years 9–12 for *P. menziesii* at the HJA site (Table 3). This suggests there was no distinguishable difference between neighbourhood interactions at different scales during that particular interval.

ALTERNATIVE EXPLANATIONS

We investigated alternative explanations for the relatively poor performance of models incorporating neighbourhood interactions as compared to models with relative dominance measures, including whether performance of the interaction indices was influenced by a mathematical artefact (i.e. using diameter vs. squared diameter, P. Couteron, personal communication) or the use of inappropriate neighbourhood sizes (Burton 1993).

Two additional interaction indices, **H′** and **L′**, were evaluated to test for a mathematical artefact due to using squared diameters (in **G** and **W**) vs. diameters (in **H** and **L**). The **H′** and **L′** indices were calculated in a similar fashion as indices **H** and **L**, but using squared diameters. With the exception of *A. rubra* in the mature stand, there was no evidence that models containing **H′** and **L′** became the best models in the set, suggesting that the mathematical transformation is not influencing our results. However, the prevalence of **L′** in the majority of best models for predicting *A. rubra* relative growth rates

Table 8 AIC_c model comparisons of selected best models using additional interaction indices for quantifying the effects of intra- and inter–specific interactions on *Alnus rubra* relative growth rates over the measurement periods examined in the mature stand (DC). **L′** was calculated in a similar fashion as index **L** but using squared diameters. For additional definitions of symbols see Table 3

Y	II	Radius	Model	K	AIC_c	Δ_i	w_i
30–35	**L′**	4.5	Intra-specific	4	−1325.9	0.00	0.27
	L′	7.5	Intra-specific	4	−1324.2	1.68	0.12
35–39	**L**	6.0	Intra-specific, interspecific, intra-X interspecific	6	−1107.5	0.00	0.22
	L′	6.0	Intra-specific, interspecific, intra-X interspecific	6	−1107.3	0.20	0.20
	L′	4.5	Intra-specific	4	−1107.1	0.39	0.19
	L′	6.0	Intra-specific	4	−1106.2	1.30	0.12
39–43	**L′**	3.0	Intra-specific	4	−1004.8	0.00	0.25
	L′	6.0	Intra-specific, interspecific, intra-X interspecific	6	−1003.3	1.50	0.12
43–47	**L**	4.5	Intra-specific, interspecific, intra-X interspecific	6	−981.7	0.00	0.17
	L	6.0	Intra-specific, interspecific, intra-X interspecific	6	−980.7	0.99	0.10
	L′	4.5	Intra-specific, interspecific, intra-X interspecific	6	−980.4	1.24	0.09
	L′	4.5	Intra-specific	4	−979.7	1.93	0.06
	L	4.5	Intra-specific	4	−979.7	1.94	0.06
	L′	6.0	Intra-specific, interspecific, intra-X interspecific	6	−979.2	1.97	0.06
47–53	**L′**	6.0	Intra-specific	4	−928.9	0.00	0.15
	L′	7.5	Intra-specific	4	−928.4	0.51	0.12
	L′	4.5	Intra-specific	4	−928.2	0.77	0.10
	L	6.0	Intra-specific	4	−927.0	1.84	0.06
	L′	9.0	Intra-specific	4	−927.3	1.91	0.06
53–56	**L**	7.5	Inter-specific	4	−886.3	0.00	0.07
	L′	6.0	Inter-specific	4	−886.2	0.14	0.07
	L	6.0	Inter-specific	4	−885.5	0.82	0.05
	L′	4.5	Inter-specific	4	−885.5	0.82	0.05
	L′	3.0	Intra-specific	4	−885.5	0.87	0.05
	L	4.5	Inter-specific	4	−885.1	1.24	0.04
	L	3.0	Intra-specific	4	−884.5	1.80	0.03
	L	9.0	Inter-specific	4	−884.3	1.99	0.03
56–68	**L′**	11.5	Intra-specific, interspecific, intra-X interspecific	6	−542.5	0.00	0.24
	L	11.5	Inter-specific	4	−541.7	0.77	0.16
	L	11.5	Intra-specific, interspecific, intra-X interspecific	6	−541.4	1.09	0.14
	L′	11.5	Inter-specific	4	−539.6	1.53	0.11

in the mature stand suggests that weighting the relative dominance of the focal tree improved our ability to predict relative growth rates (Table 8).

Results using the central trees in the CH and HJA plots had consistently indicated that the neighbourhood size was appropriate (see above). However, we also plotted the residuals from a variety of models with different neighbourhood sizes over individual tree size and found no detectable pattern (data not shown).

Discussion

The results from the three study sites support the relative dominance hypothesis, which states that the importance (*sensu* Weldon & Slauson 1986) of neighbourhood interactions varies with competitive status (i.e. size relative to the population). The differences in importance of neighbourhood interactions observed in this study appeared to be linked to changes in the relative

dominance in height of *A. rubra* and *P. menziesii* in the young and mature stands. When tree–tree interactions were occurring, neighbourhood interactions were a better predictor of individual tree growth for species with subordinate and codominant positions (i.e. heights) in the population, whereas expressions of relative dominance (i.e. tree size relative to the population) were better predictors of individual tree growth for species with dominant heights. The results of this study suggest that interactions were perfectly size-symmetric (*sensu* Schwinning & Weiner 1998), thus linking the size of a tree relative to the population to its resource capturing capacity (Ford & Diggle 1981; Miller & Werner 1987; Goldberg 1990). Obviously, the relationships predicted by the relative dominance hypothesis only apply to conditions in which plants are interacting and will not hold true in low density stands of small plants, such as those observed over the earliest measurement period in the young stands.

While other studies investigating species interactions have been limited to investigations of shorter time periods, their findings also support the relative dominance hypothesis. For example, in another conifer/broadleaf mixture, the taller tree species, *Liquidambar styraciflua*, had a significant effect on the resources available to the subordinate species, *Pinus taeda*, whereas *P. taeda* did not significantly affect the resources available for *L. styraciflua* (Zutter *et al*. 1997). These findings suggest that the size of the dominant species, *L. styraciflua*, relative to the population was the most important factor determining its growth, whereas the growth of the subordinate species, *P. taeda*, was strongly affected by the neighbouring *L. stryraciflua*. Similar results were also found in a removal experiment of herbaceous and grassy species, in which the growth of the tallest species, *Plantago lanceolata* and *Sanguisorba minor*, were not significantly affected by competition from the subordinate species, *Briza media*, *Carex caryophllea* and *Lotus corniculatus* (McLellan *et al*. 1997). In addition, longer-term studies of neighbourhood competition have also noted that individual tree sizes, rather than neighbourhood conditions, become better predictors of growth as over time the height of the focal species increasingly exceeds the height of the neighbouring vegetation (e.g. Wagner & Radosevich 1998).

Studies that investigated aspects of this phenomenon in monocultures also support the relative dominance hypothesis and suggest that this hypothesis may also apply to individuals within a population. For example, Cannell *et al*. (1984) noted a weak relationship between measures of neighbourhood interactions and the relative growth rates of individuals with dominant heights in monocultures of *Picea sitchensis* and *Pinus contorta*. Competitive status, as quantified by height relative to the population, was able to explain significantly more variation in the growth of dominant individuals than measures of neighbourhood interactions (Cannell *et al*. 1984). Also, an examination of size hierarchy development in monocultures of *Tagetes*

patula found that the dominant individuals in the population all shared higher relative growth rates (Ford 1975). On the other hand, there was a great deal of variation in relative growth rates among subordinate individuals (Ford 1975). These independent findings from a variety of species and study conditions all fit within the predictions of the relative dominance hypothesis, confirming that dominant plants were less affected by neighbourhood interactions than subordinate individuals.

The strong relationships between relative dominance and the growth of dominant individuals observed in this and other studies are presumably due to the greater access to available resources for a plant of a dominant size, i.e. due to a competitive advantage. In this study, the inherent height growth patterns of *A. rubra* and *P. menziesii* resulted in each species having a height advantage at a different stage of development. Within the constraints of inherent growth patterns, trees with greater heights (i.e. a size advantage) at a given point in stand development appear to have greater access to available resources (Connolly & Wayne 1996) and were thus less affected by neighbourhood interactions. However, the interactions were size-symmetrical (*sensu* Schwinning & Weiner 1998), indicating that the differences in performance were directly proportional to size differences. This pattern was found for both species and in both the young and mature stands.

It is important to recognize the limitations of the methods used in this study for testing the relative dominance hypothesis (e.g. Thomas & Weiner 1989). At the CH and HJA study sites, the relative dominance interaction indices may have been performing similarly to a neighbourhood interaction index due to the small plot sizes. However, the strong relationships between tree growth and neighbourhood interaction indices using 3.0 and 4.5 m neighbourhoods in several of the measurement periods, along with the results of the tests using the central trees at each site, suggest that interactions with first order neighbours were most important. In addition, the mean crown diameter estimates for these sites over the periods examined (2.6, 3.8, and 4.3 m at years 6, 9, and 12, respectively, at the CH study site and 1.6, 3.3, and 3.9 m at years 6, 9, and 12, respectively, at the HJA study site) also suggest that interactions were occurring primarily with direct neighbours. For the DC study site, the lack of a complete census of tree heights limits our ability to reach unequivocal conclusions on their relative dominance although the similarity between the trends in D and height (Fig. 1c) over time suggest that similar patters are also valid in this stand (Fig. 1c).

As with limitations due to neighbourhood sizes, the use of inappropriate measures of neighbourhood interactions (Thomas & Weiner 1989) could not explain our results. We used a variety of measures and statistically selected the best fitting models. Also, while the layout of the studies were not optimal for testing the importance of including inter–tree distances in interaction indices, the significance of the strong relationships between neighbourhood interactions and tree

growth in the majority of measurement periods suggested that we included the most appropriate measures of neighbourhood interactions. We therefore believe that relative dominance, expressed in tree height, is likely to drive the trends observed.

Conclusions

Results from three different mixed species stands supported the relative dominance hypothesis and demonstrate the influence of relative dominance on the importance of neighbourhood interactions in forest communities. While other authors have recognized the importance of accounting for the social status of individual trees when predicting growth (Tomé & Burkhart 1989; Dhôte 1994), the results of our study provide a framework for future work evaluating the relationship between relative dominance and the importance of neighbourhood competition. Although a two-species mixture was used in this study, it is likely that the relationships predicted by the relative dominance hypothesis are appropriate for individuals within a population and for communities composed of numerous species. The documentation of similar trends in perennial plant communities, suggests that the application of this hypothesis may not be restricted to interactions between tree species. The relationships between relative dominance in height and neighbourhood interactions described here are presumably due to the importance of competition for light, but alternative measures, such as rooting depth (e.g. Manning & Barbour 1988), may be needed in environments in which competition for below-ground resources is more important.

Acknowledgements

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Klaus J. Puettmann · Mike R. Saunders

Patterns of growth compensation in eastern white pine (*Pinus strobus* L.): the influence of herbivory intensity and competitive environments

Abstract To investigate complex growth compensation patterns, white pine (*Pinus strobus* L.) seedlings were clipped to simulate different herbivory levels. Seedlings were growing with different understory competition levels (created through monthly weeding vs no brush control) under a range of overstory canopy closures. Compensation patterns varied for the different growth and size measures. After one growing season, seedlings did not fully compensate for lost biomass regardless of the competitive environments of the seedlings. Although relative height growth was stimulated by light intensity clipping (20–40% of last-year shoots removed), relative diameter growth, total biomass, and biomass growth of seedlings declined sharply with increasing clipping intensity. Likewise, all growth parameters declined with increasing interspecific competition. Results showed that seedlings in highly competitive environments showed smaller growth loss due to clipping than those in competition-free environments, presumably because seedlings experiencing high interspecific competition devoted more energy to maintaining apical dominance and a balanced shoot-root ratio. While competition from canopy trees altered compensatory patterns, competition from understory vegetation only altered the magnitude, but not the patterns, of compensatory growth. We suggest that compensatory growth follows a complex pattern that will vary with the parameters measured, competitive conditions, and clipping intensities. Our results support the assertion that overcompensation may be an adaptation to competitive ability, rather than a response to herbivory itself.

Introduction

Plants have developed a variety of chemical and physical defenses to discourage browsing by mammals (Strauss and Agrawal 1999). Often, these defenses reduce the palatability of the plant, usually either by preventing access to the plant (i.e., thorns) (Myers and Bazely 1991) or by reducing the nutritional value of the plant matter [i.e., increasing the lignin content of the tissue or introducing secondary metabolites that specifically interfere with digestion of the plant (Bryant et al. 1991a, 1991b, 1992)]. Plants also may display "alternative defense traits" (Strauss and Agrawal 1999). Such traits may include a plant's increased ability to reproduce and/or regrow after herbivory. This phenomenon, called tolerance to herbivory or compensatory growth, was first suggested by Dyer (1975) and is fairly well documented for grass dominated ecosystems (McNaughton 1979; Detling and Painter 1983; Du Toit et al. 1990; Frank and McNaughton 1993; Painter and Belsky 1993). This phenomenon has also been proposed for woody perennials (Belsky 1987; Hjältén et al. 1993; Canham et al. 1994), but has been found to be species and study specific. Several authors suggest that overcompensation is more likely in environments with high moisture and nutrient availability (e.g., Maschinski and Whitham 1989), while others found the opposite effect (e.g., Mutikainen and Walls 1995). The degree of compensation was also influenced by timing of herbivory and competition. Generally, plants seem more likely to overcompensate after early season herbivory (Maschinski and Whitham 1989) and in areas with low competition (Maschinski and Whitham 1989; Irwin and Aarssen 1995). Alternatively, many authors have found the herbivore-plant relationship to be either antagonistic, i.e., any level of herbivory results in reduced plant vigor (e.g., Ehrlich and Raven 1964; Levin 1976; Crawley 1983; Marquis 1984; Rhoades 1985; Zimov et al. 1995),

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or to follow a threshold model, i.e., herbivory does not affect plant growth and fitness until a threshold level of herbivory is reached (McNaughton 1979; for examples see Linzon 1958; Roy 1960; Metzger 1977; Pastor et al. 1988; Gill 1992).

Most papers supporting the compensatory plant growth hypothesis used a broad definition that referred to any positive response of the plant to injury as compensatory growth (Belsky 1986, 1987). Belsky (1986, 1987) suggested that the use of the term be limited to measures of dry weight and defined overcompensation, exact compensation, and undercompensation as when the cumulative dry weight (including removed tissue) of the grazed or clipped plants was greater, the same, or less than the total dry weight of the control plants, respectively. Other authors define overcompensation as when damaged plants having a greater fitness than undamaged plants (Strauss and Agrawal 1999). Thus, inconsistencies in interpretation of the pattern of plant response to herbivory and compensatory growth may be due to the differences in the measure (e.g., height, diameter or biomass) and the specific study conditions (Belsky 1986; Strauss and Agrawal 1999). To sort out some of these inconsistencies, we present the results from an experimental study that analyzed different measures of compensatory growth with regard to variable herbivory intensity and competitive conditions.

Eastern white pine (*Pinus strobus* L.) is a coniferous, mid-successional species that shows deterministic growth from terminal clusters of buds on the parent shoots (Wilson 1992). It is an important component of the diet of white-tailed deer (*Odocoileus virginianus* Zimmermann), especially in late winter/early spring before the vegetation "greens up" in the Lake States, and is of great commercial, wildlife, and aesthetic value. To simulate typical herbivory patterns (Hjältén et al. 1993; but see Baldwin 1990), we clipped white pine seedlings at several different intensities and under a range of competitive conditions in early spring and measured various aspects of growth response after one growing season. We addressed the following questions: How do (1) intensity of herbivory and (2) overstory and understory competition affect the compensatory growth responses of white pine seedlings herbivory? (3) How do different measures of compensatory growth or size (e.g., height, diameter, biomass) compare in their relationship to intensity of herbivory and competition? (4) Can a shift in biomass allocation patterns explain these relationships?

Materials and methods

Site description

This experiment was conducted in a 45-year-old jack pine plantation located 15 km southeast of Grand Rapids, Minnesota, in southern Itasca County (approximately 47°E 7′ N, 93°E 22′ W). The 9.5 ha site lies on a level, upland area formed from a glacial outwash plain and is 390 m above sea level. The soil type is predominately Menahga-Graycalm sandy outwash consisting of 70% sand, 20% silt, and 10% clay (unpublished data).

In 1994, the site was partially harvested using a combination of a 2.8 ha clear-cut (southeastern corner of plantation) and 6-m-wide strip-cuts (rest of plantation). This removed the overstory on approximately 50% of the site. Within the strip-cut area of the plantation, overstory basal area (BA) and cover ranged from 6 m^2/ha and 51% in strip cuts to 36 m^2/ha and 89% under the residual overstory. Understory cover was relatively sparse (0–40% cover) under residual canopy but increased dramatically within the strips and clear-cut areas (50–100% cover). Predominant understory species included bracken fern [*Pteridium aquilinum* (L.) Kuhn.], raspberry and blackberry (*Rubus* spp.), beaked hazel (*Corylus cornuta* Marsh.), chokecherry (*Prunus virginiana* L.), and aspen sprouts (*Populus* spp.).

Experimental design

During the spring of 1996, 720 3–0 white pine seedlings were planted at 1.0-m spacing within 17 plots located across the site. To ensure a range of overstory competitive conditions, two plots consisted of 90 (9 rows×10 seedlings/row) seedlings each; these were open and closed controls and located within the clear-cut and an uncut portion of the jack pine stand. The remaining plots had 36 seedlings (9 rows×4 seedlings/row) and were clustered into groups of three, for a total of five clusters across the strip-cut portion of the site. Within each cluster, one plot was located in the center of a cut strip, one was located on the edge of the cut strip under the residual overstory, and one was located in the center of an uncut strip. This provided relatively open (BA=10.3±1.1 m^2/ha (mean±SE)), intermediate (BA=22.7±3.1 m^2/ha), and closed canopy conditions (BA=31.0±2.4 m^2/ha).

Within each plot, seedlings were either weeded monthly (MON) to remove all herbaceous and woody competitors, weeded annually (ANN) to reduce cover of herbaceous competitors and remove most woody competitors, or never weeded (CTRL). Weeding treatments were randomly applied to entire rows of seedlings (4 or 10 seedlings) under the restrictions that (1) control and monthly weeding treatments could not occur in adjacent rows; and (2) the same weeding treatment could not occur in three adjacent rows. MON was applied monthly throughout 1996 and 1997 growing seasons; ANN was applied twice, in June 1996 and June 1997.

In late April and early May 1997, seedlings were assigned to one of following clipping classes: an unclipped control or the removal of the terminal and approximately 25%, 50%, 75%, or 100% of last year's shoots. To avoid artificially dispersing clipping damage throughout the crowns of the seedlings (see Edenius et al. 1993), we clipped in 1, 2, or 3 adjacent quadrants for the 25%, 50%, and 75% treatments, respectively. This distributed clippings vertically on the seedlings and, in cases where laterals were concentrated on one side of the seedling, allowed quadrants to be expanded or narrowed as needed to achieve desired clipping intensities. The timing and clipping patterns were chosen to approximate natural deer browsing as close as possible and clipping classes were used to ensure a broad range of actual clipping intensities. Two complete replications of clipping classes were installed in each weeding treatment in the 9×4 plots and three complete replications were installed in the 9×10 plots.

Field measurements

Total height, basal diameter at 1 cm above the ground, the number of last-year lateral branches in the primary flush, and number of last-year lateral branches overall were recorded for each seedling. For clipped seedlings, the number of last-year branches removed was also recorded. Seedlings were measured before clipping in April 1997 and after growth had stopped in October 1997.

To expand beyond an earlier study (Saunders and Puettmann 1999), which was limited to measuring height and diameter response, and investigate compensatory growth sensu Belsky (1986) (i.e., with total biomass, including removed plant parts), we col-

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Table 1 Models used to estimate initial biomass values of fall 1997, harvested seedlings. Models were developed from unclipped seedlings harvested before budbreak in spring 1997

*$P<0.05$
**$P<0.01$

Initial biomass model: $Y=\alpha\,(HT_{ini,bc})^{\beta}\,(DIA_{ini})^{\delta}$	n	Parameter			MSE	F	P	R^2_{ADJ}
		α	β	δ				
Aboveground	65	0.091**	0.251*	2.067**	1.586	208.97	<0.001	0.867
Leaves	65	0.083**	0.141[ns]	2.038**	0.926	111.17	<0.001	0.775
Stems	65	0.017**	0.453**	2.083**	0.191	334.18	<0.001	0.912
Belowground	41	0.082**	0.336*	1.408**	0.332	67.62	<0.001	0.769
Total	41	0.162**	0.231[ns]	1.958**	2.329	197.58	<0.001	0.908

lected all clipped material and harvested some seedlings and their roots before the experiment began and some after one growing season. In April 1997, we harvested 41 randomly selected unclipped seedlings to model initial biomass of all treated and untreated seedlings. To estimate final seedling biomass, we harvested a total of 91 seedlings (14–21 seedlings from each clipping class) in October 1997; these were randomly selected from all available seedlings within the CTRL and MON weeding treatments. All clippings and harvested seedlings were labeled and, upon returning to the laboratory, stored in a freezer at –16°C. As soon as possible, samples were removed from the freezer, cleaned of foreign matter and soil, and put in a drying oven for 72 h at 70°C. After being removed from the oven, samples were separated into roots, stems, and needles and immediately weighed to the nearest 0.001 g using a digital scale.

In late July 1997, overstory canopy structure above each seedling was measured with the LICOR LAI-2000 Plant Canopy Analyzer. Readings were taken with two instruments. One was placed in an adjacent open area to measure "above canopy" conditions. The second measured light levels immediately above each seedling. Both readings were taken when the skies were completely overcast or when solar elevations were low (i.e., the early morning and late evening). A 270° view lens cap restricted the view of the instruments from a 90° arc; this allowed the operator to "hide" from the instruments. Similarly, readings were restricted to a 43° cone to reduce the influence of sun flecks on measurements that might otherwise negatively bias the results (Chason et al. 1991; Grantz et al. 1993; Strachan and McCaughey 1996). The readings from both instruments were integrated to calculate DIFN, an indicator of "canopy openness" (LI-COR 1992; Puettmann and Reich 1995; Saunders and Puettmann 1999) that has been shown to be related to light availability (Gendron et al. 1998). Overstory canopy closure (OCC) was then calculated as:

$$OCC\,(\%)=(1-DIFN)\times100 \tag{1}$$

and average plot values for OCC were calculated.

Statistical analyses

Statistical analyses were conducted on (1) relative height growth, (2) relative diameter growth, (3) absolute above ground, below ground and total biomass growth and (4) needle, stem, root, and total biomass of seedlings after one growing season. All analyses used actual clipping intensity (CLIP) as a variate, as defined by the proportion of last-year shoots including the terminal, removed during the clipping treatment. This approach was taken because it was difficult to remove exactly 25%, 50%, or 75% of last-year shoots; these young seedlings often had only a few last-year shoots and treatments would sometimes remove more or less than the desired percentage of shoots (e.g., a 25% clipping could remove at least 33% of last-year shoots if only two laterals and one terminal were present on the seedling).

Analyses for (1) and (2) were conducted on relative growth instead of absolute growth since the growth of a tree is related to its initial size (Puettmann and Reich 1995). Relative height growth (RHG) was defined as:

$$RHG=(HT_{fin}-HT_{ini,\,ac})\,/\,HT_{ini,\,bc} \tag{2}$$

where HT_{fin} is final seedling height, $HT_{ini,\,ac}$ is initial seedling height after clipping, and $HT_{ini,\,bc}$ is initial seedling height before clipping. Relative diameter growth (RDG) was defined as:

$$RDG=(DIA_{fin}-DIA_{ini})\,/\,DIA_{ini} \tag{3}$$

where DIA_{fin} is final seedling diameter and DIA_{ini} is initial seedling diameter. Effects of competing vegetation and clipping on relative growths were tested using a weighted analysis of covariance (ANCOVA), with OCC and CLIP as covariates and the weeding treatment (WEED) as a factor. In order to reduce heteroscedasticity in the ANCOVA model, the natural logarithms of RDH and RDG were used in analysis as suggested by the Box-Cox transformation testing procedure (Neter et al. 1983).

In this study, total biomass (BIO_{tot}) was defined as the cumulative dry weight of a seedling including removed (i.e., clipped) tissue or:

$$BIO_{tot}=BIO_{fin}+BIO_{clip} \tag{4}$$

where BIO_{fin} is the dry weight of the seedling after one growing season and BIO_{clip} is the dry weight of material removed during the clipping treatment (Belsky 1986). Stem (BIO_{stem}), root (BIO_{root}) and needle (BIO_{needle}) biomass were calculated using the same approach. Total, above, and below ground biomass growth (BG_{total}, BG_{above}, and BG_{below}) could not be defined in terms of measurable parameters. Therefore, initial biomass (BIO_{ini}) of fall-harvested seedlings had to be modeled from the biomass of spring-harvested seedlings using non-linear least squares regression. Models for each plant component are presented in Table 1. BGs could then be parameterized as:

$$BG=BIO_{fin}-BIO_{ini} \tag{5}$$

To isolate the effects of competition and clipping on the various BIOs and BGs, unweighted ANCOVA analyses were conducted using OCC and CLIP as variates and WEED as a factor (with only two levels – no weeding and monthly weeding). To reduce heteroscedasticity in the BIO and BG models, response variables (y_o) were transformed by: $y=\ln(y_o+b)$, with constant ($b=10$) included in only the BG models to avoid undefined values (i.e., $y_o=0$).

Interaction among variates and factors in all ANCOVA models was tested using sequential sums of squares and F-ratios. Comparisons among treatment means were tested using the Tukey honestly significant difference (HSD) to control for experiment-wise type I errors (Kuehl 1994). All tests were considered significant if $P<0.05$ and marginally significant if $P<0.10$. All statistical analyses were calculated with JMP 3.2.1 (SAS 1996) and SPSS 6.3.1.

Results

In general, the compensatory patterns differed between growth measures and were influenced by the treatments and study conditions. Specifically, clipping intensity (CLIP) significantly influenced compensatory patterns of

A.

Relative Height Growth

B.

Relative Diameter Growth
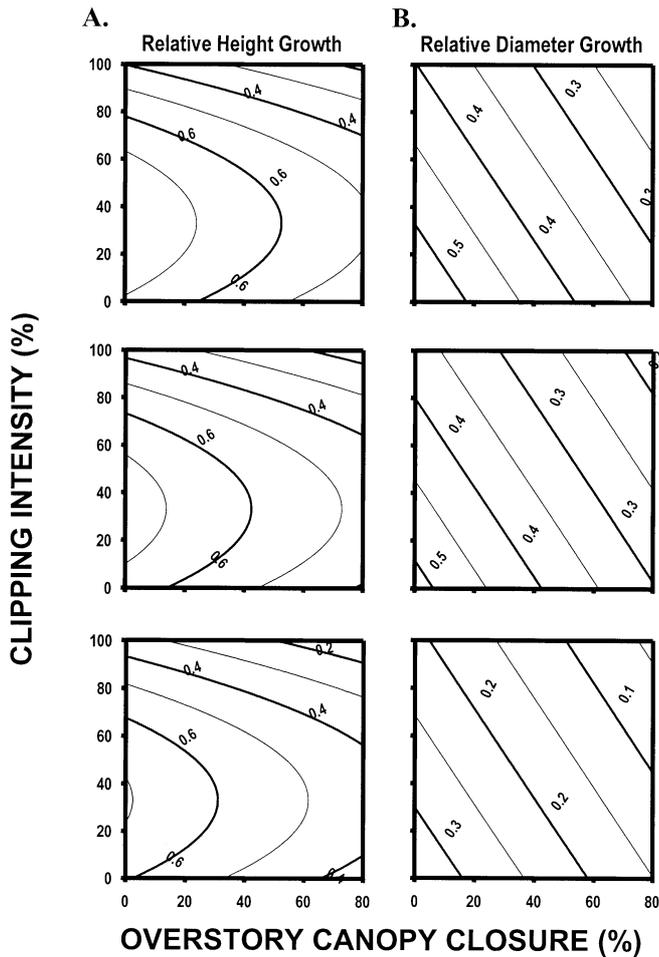
Fig. 1 Contour plots of relative height (**A**) and diameter (**B**) growth models as a function of overstory canopy closure (*OCC*) and clipping intensity (*CLIP*) for the three different weeding (*WEED*) treatments. Weeding treatments included monthly weeding (*top*), annual weeding (*middle*) and control (*bottom*). Clipping intensity is measured as the proportion of last-year shoots, including terminal, removed. Relative growth was calculated according to Eq. 2

Table 2 Analysis of covariance for the effects of initial biomass (by component), overstory canopy closure (*OCC*), percentage of last-year shoots removed (*CLIP*), and understory brush treatments (*BRUSH*) on final biomass of fall 1997, harvested seedlings. Initial biomasses were calculated from equations in Table 1

| Source	df	MSE	F	P
Final leaf biomass (g)[a]				
INILEAF[a]	1	9.345	59.307	<0.001
OCC	1	4.735	30.050	<0.001
CLIP	1	4.257	27.019	<0.001
OCC×CLIP	1	1.369	8.688	0.004
BRUSH	1	4.856	30.816	<0.001
ERROR	83	0.158		
Final stem biomass (g)[a]				
INISTEM[a]	1	14.848	114.848	<0.001
OCC	1	3.011	23.289	<0.001
CLIP	1	3.495	27.034	<0.001
OCC×CLIP	1	1.141	8.824	0.004
BRUSH	1	4.276	33.072	<0.001
ERROR	83	0.129		
Final root biomass (g)[a]				
INIROOT[a]	1	7.702	69.486	<0.001
OCC	1	1.684	15.192	<0.001
CLIP	1	0.692	6.242	0.015
OCC×CLIP	1	0.419	3.782	0.055
BRUSH	1	1.966	17.734	<0.001
ERROR	83	0.111		
Final total biomass (g)[a]				
INITOTAL[b]	1	9.908	98.359	<0.001
OCC	1	3.148	31.249	<0.001
CLIP	1	2.652	26.330	<0.001
OCC×CLIP	1	1.011	10.041	0.002
BRUSH	1	3.478	34.528	<0.001
ERROR	83	0.101		

[a] To stabilize variances, model was linearized with a natural logarithm transformation
[b] Transformed by natural logarithm to maintain scale

relative height growth. The relationship between relative height growth and CLIP was quadratic ($P<0.001$), with relative height growth greatest when approximately 30% of the last-year shoots were removed (Fig. 1). At higher clipping intensities, the benefit of clipping declined and at the highest clipping intensity (100% of last year shoots removed) the seedlings were undercompensating. However, since we also removed the terminal, this growth stimulation at low to intermediate clipping intensities did not result in trees that were taller than trees in the controls after one growing season. For example, as averaged across all overstory conditions and weeding treatments, unclipped trees were 40.0±0.9 cm (mean±SE) in height, while trees with 20–40% of last-year shoots removed were only 31.4±1.6 cm tall.

Unlike relative height growth, relative diameter growth showed undercompensation at any clipping intensity. The degree of undercompensation was linearly related to the clipping intensity ($P<0.001$, Fig. 1). There-

fore, clipping at any intensity reduced final seedling diameter; unclipped trees averaged 6.44±0.16 mm in diameter, while trees with 40–60% of last-year shoots removed and 100% of last-year shoots removed averaged 5.95±0.15 mm and 5.80±0.24 mm, respectively. There were no interactions between CLIP and either OCC or WEED for either relative height growth or relative diameter growth ($P>0.10$). This suggested that height and diameter growth were affected only additively in the short term (i.e., one growing season) by the multiple stresses imposed on the seedlings.

Clipping intensity also significantly influenced total final biomass (Table 2) and total biomass growth (Table 3) of harvested seedlings. Total seedling biomass dramatically decreased with increasing clipping intensity (Table 2, Fig. 2a). For example, seedlings with 40–60% and 100% of last-year shoots removed averaged 74% and 64%, respectively, of the biomass of unclipped seedlings. Likewise, clipping at any intensity reduced biomass growth of seedlings (Table 3, Fig. 2b). Biomass growth declined from 6.53±1.57 g/year in unclipped

Fig. 2 Contour plots of final biomass (**A**), biomass growth (**B**), and shoot/root ratio (**C**) models (see Tables 3, 4) as a function of overstory canopy closure (*OCC*) and clipping intensity (*CLIP*) for unweeded seedlings and seedlings with monthly brush control. Graphs in **A** are for final leaf, stem, root, and total biomass (top to bottom), in **B** for aboveground, belowground and total biomass growth (top to bottom). Numbers on the contours are grams and grams/year for plot (**A**) and (**B**), respectively, or the ratio of the aboveground biomass to below ground biomass (**C**). Clipping intensity is measured as the proportion of last-year shoots, including the terminal, removed from the plant

CLIPPING INTENSITY (%)

OVERSTORY CANOPY CLOSURE (%)
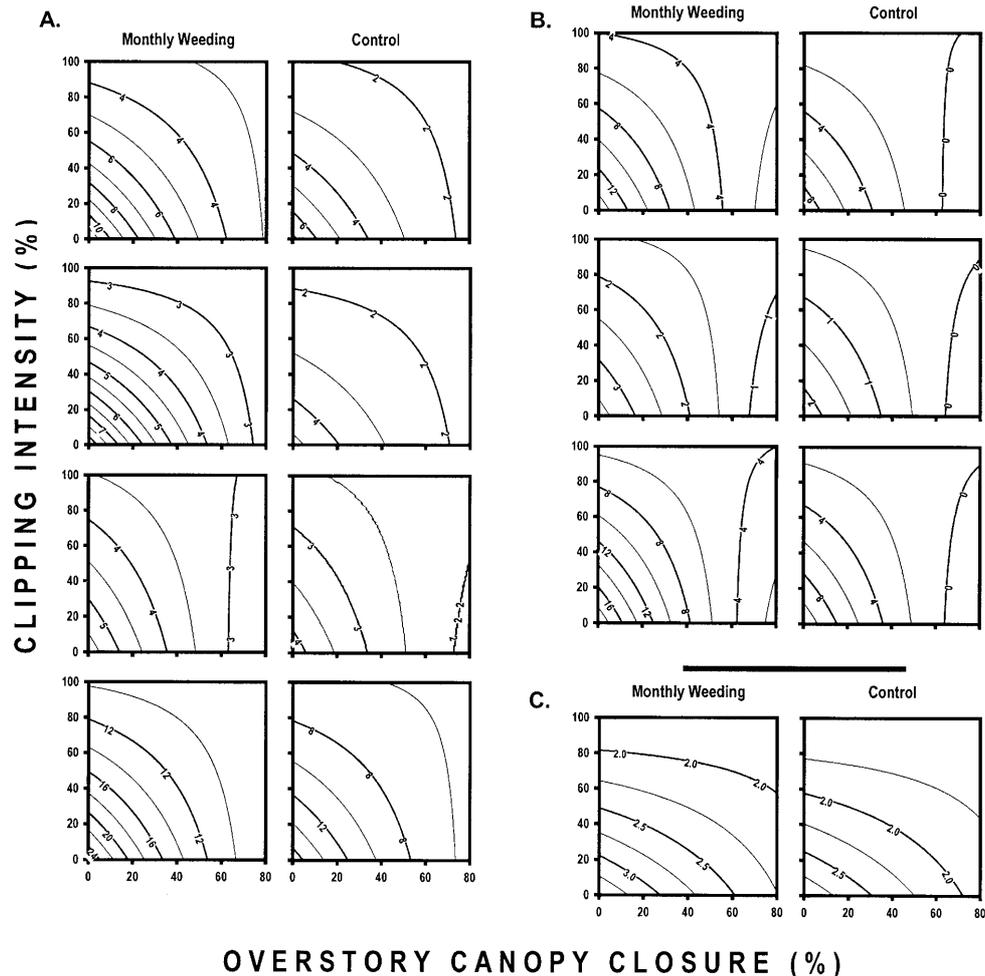
Table 3 Analysis of covariance for the effects of overstory canopy closure (*OCC*), percentage of last-year shoots removed (*CLIP*), and understory brush treatments (*BRUSH*) on biomass growth of fall 1997, harvested seedlings. Biomass growth was calculated as the difference between the final, measured biomass and an estimated, initial biomass using equations from Table 1

Source	*df*	MS	*F*	*P*
Above ground biomass growth (g/year)[a]				
OCC	1	1.755	46.828	<0.001
CLIP	1	0.980	26.125	<0.001
OCC×CLIP	1	0.597	15.924	<0.001
BRUSH	1	1.481	39.512	<0.001
ERROR	84	0.037		
Below ground biomass growth (g/year)[a]				
OCC	1	0.167	17.698	<0.001
CLIP	1	0.081	8.619	0.004
OCC×CLIP	1	0.053	5.649	0.020
BRUSH	1	0.248	26.339	<0.001
ERROR	84	0.009		
Total biomass growth (g/year)[a]				
OCC	1	2.266	40.657	<0.001
CLIP	1	1.184	21.245	<0.001
OCC×CLIP	1	0.762	13.677	<0.001
BRUSH	1	2.171	38.949	<0.001
ERROR	84	0.056		

[a] To stabilize variances, model was linearized with a natural logarithm transformation

seedlings to 2.63±1.31 g/year in seedlings with 40–60% of last-year shoots removed and to 1.71±0.97 g/year in seedlings with 100% of last-year shoots removed. However, unlike relative height and diameter growth, the OCC×CLIP interaction was marginally significant in the total biomass model and highly significant in the total biomass growth model (Tables 2, 3). In general, biomass compensatory patterns of seedlings under dense canopies (i.e., high OCC) were not affected as greatly by increasing clipping intensity as of seedlings in open, unshaded environments (a low OCC; Fig. 2). For example, seedlings with 100% of last-year shoots removed averaged only 14% of the biomass growth of unclipped controls when OCC was between 0–25%, while they averaged 93% of the biomass growth of unclipped controls when OCC was 50–75%. Thus, white pine seedlings may exhibit exact compensation under denser overstory conditions and undercompensation under more open conditions. No other interactions were significant in final biomass or biomass growth models.

Overstory competition had significant effects on the relative growth rates of seedlings but not necessarily on the patterns of compensatory growth. While the patterns (over- vs exact vs under-compensation) were not altered by OCC, the absolute amount of growth reduction increased with increasing overstory density (*P*<0.001 for

Table 4 Final height, relative height growth, final diameter, and relative diameter growth of seedlings as summarized by understory weeding treatment. Weeding treatments included an unweeded control (*CTRL*), an annual weeding of woody competitors (*ANN*), and a monthly weeding of woody and herbaceous competitors (*MON*). Values in each column with the same letter are not significantly different from each other (*P*<0.05, Tukey-Kramer HSD test)

Understory weeding treatment	n	Final height (cm)	Relative height growth	Final diameter (mm)	Relative diameter growth
CTRL	85	29.8[a]	0.439[a]	5.29[a]	0.182[a]
ANN	85	31.3[a]	0.475[a]	6.34[b]	0.348[b]
MON	85	32.4[a]	0.504[a]	6.60[b]	0.359[b]

relative height and relative diameter growth). On the other hand, the pattern of biomass compensatory growth in relationship to clipping intensity varied between seedlings grown under different overstory conditions (see above).

Weeding treatments were also influential (Table 4) in determining the amount of growth. Generally, monthly weeded seedlings (MON) grew slightly better than annually weeded seedlings (ANN) and significantly better than unweeded controls (CTRL) (*P*=0.008 and *P*<0.001 for relative height and relative diameter growth, respectively,. For total biomass and total biomass growth, the difference between MON and CTRL was quite large, e.g., monthly weeding increased total final biomass by 86% and biomass growth by 864% over unweeded seedlings. Weeding treatments did not alter the compensatory patterns for any of the growth measures tested, however.

Biomass allocation was influenced by competitive conditions and clipping intensity. While the compensatory patterns described for total biomass and total biomass growth are consistent for all biomass components (Tables 2, 3), the absolute amounts of growth response were not identical (Fig. 2a, b). Thus, the shoot/root ratio, defined as aboveground biomass divided by below ground biomass, shows that biomass allocation varied with study conditions. Increased clipping intensity resulted in seedlings with a lower shoot/root ratio (Fig. 2c), although this effect was partially a result of the clipping treatments themselves (i.e., shoot biomass was artificially reduced by clipping in the spring and trees were still responding to it). Likewise, increasing OCC reduced the shoot/root ratio (Fig. 2c). On the other hand, the shoot/root ratio for seedlings in unweeded, control plots was lower than for seedlings in plots that received monthly weed control. For example, average shoot/root ratio for unweeded and weeded seedlings was 1.94±0.09 and 2.41±0.13, respectively.

Discussion

This study shows the complexity of plant compensatory growth response patterns. It pointed out that many factors influence white pine seedlings' responses to simulated herbivory, which may explain why general patterns regarding compensatory growth are hard to establish (Strauss and Agrawal 1999). For example, low intensity clipping stimulated relative height growth, while relative diameter growth, biomass growth, and final total biomass of seedlings declined at any clipping intensity. Typically, height growth is the most likely to exhibit overcompensation in hardwood (Hjältén et al. 1993; Canham et al. 1994; Shabel and Peart 1994; McLaren 1996) and conifer species (Mitscherlich and Weise 1982), including white pine (Wilson 1992; Saunders and Puettmann 1999). On the other hand, other studies did not find overcompensation in height growth in several hardwood species (e.g., Metzger 1977; Canham et al. 1994) and in conifer species when leaders were not removed (Mayhead and Jenkins 1992; Bergström and Danell 1995).

Diameter growth response seems to show a consistent pattern of undercompensation in hardwood (Braithwaite and Mayhead 1996) and conifer species (Mitscherlich and Weiss 1982; Mayhead and Jenkins 1992). The dichotomy in height and diameter growth responses is common in white pine; in a similar study, we observed that white pine showed compensatory height growth at medium clipping levels, but did not show compensatory diameter growth during the growing season immediately after clipping (Saunders and Puettmann 1999).

The response to herbivory in terms of biomass (overcompensation sensu Belsky 1986) has been investigated less frequently for woody plants. Our study supports an antagonistic plant–herbivore relationship, i.e., any level of herbivory will lead to reduced biomass growth and reduce total final biomass. Our results also support the hypothesis that compensatory height growth is, at least partially, a result of significant shift in biomass allocation from diameter growth and root growth within the plant. This agrees with Belsky's (1986) assertion that herbivory is a cost to the plant, and that regrowth to replace lost aboveground tissues will reduce below ground growth and deplete stored plant reserves (Mabry and Wayne 1997).

While all plant components (above and below ground biomass as well as root, stem, and leaf biomass growth) followed a similar trend, the absolute growth response among plant components was different resulting in a decreased shoot/root ratio for clipped seedlings, a trend also found for sitka spruce [*Picea sitchensis* (Bong.) Carr.] (Mayhead and Jenkins 1992) and non-woody plants (e.g., Welter and Steggal 1993). On the other hand, defoliation or disbudding of several annual and biennial species led to a shift in biomass allocation from roots to shoots (e.g., Mabry and Wayne 1997; Julien and Bourne 1986; Richards 1984). This trend was attributed

to reestablishment of leaf canopies and shoot/root balances (Richards 1984) or – in nutrient-limiting environments – to root mortality (Chapin and Slack 1979). In natural settings, other factors, like fertilization by the herbivores, may have resulted in the overcompensation in aboveground biomass of grass species (Hik and Jefferies 1990), even though the phenomenon also has been documented in experimental settings regardless of nutrient status (e.g., Wegener and Odasz 1997).

This study's response may be partially due to a size effect, as bigger plants usually have a higher shoot/root ratio (Johnson 1990). On the other hand, the influence of interspecific competition on biomass allocation within this study was consistent with the general trend that shoot/root ratios for trees increase in lower competitive environments (Wang et al. 1994; Mitchel and Arnott 1995).

Our study indicated that the question whether compensation is more likely under high or low competitive conditions (Strauss and Agrawal 1999) is too general and different competitive conditions need to be distinguished. Competition from overstory trees and understory vegetation appeared to affect seedlings differently. Increased overstory competition resulted in slower growth, but reduced the impacts of clipping, i.e., compensatory patterns in terms of total biomass growth shifted from under-compensation to exact compensation at low clipping intensities. Monthly weeding that removed woody perennials and herbaceous competitors increased growth significantly compared to controls, but did not influence the compensatory patterns. Results from this study suggest that seedlings in open, non-competitive environments are most affected by herbivory in absolute terms. Apparently, herbivory stress results in relatively smaller growth losses when plants are growing slowly due to competitive conditions. Edenius et al. (1993) and others concluded that overcompensation was not a specific adaptation to herbivory, but an indirect consequence to make up for lost competitive status (Belsky 1986; Edenius et al. 1993; Hjältén et al. 1993; McLaren 1996). Thus, compensatory growth may not be as advantageous, and therefore less pronounced, in less competitive environments. While this trend has been observed for a variety of other tree species (Hjältén et al. 1993; McLaren 1996), it does not suggest that seedlings in non-competitive environments can recover easily from herbivory losses, particularly when the intensity and frequency of browsing is high (McLaren 1996; Saunders and Puettmann 1999). This may possibly be due to the increasing necessity for apical dominance and maintaining a balanced shoot-root ratio in highly competitive, shady environments (McLaren 1996).

The compensatory height growth pattern may be explained by the competitive advantage of establishing apical dominance as quickly as possible (Aarson and Irwin 1991; Mutikainen and Walls 1995). A plant that concentrates its resources on increasing leader length would more likely over-top potential competitors and thus increase chances of long-term survival. On the other hand,

if a plant is not in danger of being over-topped, this response may not necessarily lead to better survival when other stresses affect plants. For example, if seedlings in a competitive environment use much of their reserves to compensate for lost foliage, they might exhibit an unbalanced shoot-root ratio and thus maybe more sensitive to future episodes of herbivory or drought periods (Hjältén et al. 1993; see also Messier et al. 1999).

Lastly, it is important to note that any response to herbivory may only be temporary. For example, by the second growing season following clipping, surviving trees had the same aboveground growth as control trees regardless of clipping intensity and competitive conditions (McLaren 1996; Saunders and Puettmann 1999), presumably because newly formed terminals had re-established apical control within the plant (Hjältén et al. 1993; Chamberlin and Aarssen 1996). Also, note that this study used hand clipping as treatment, rather than actual herbivore browsing. While growth effects of herbivore saliva have been documented in some greenhouse studies (e.g., Reardon et al. 1972), these effects could not confirmed in field studies (e.g., Reardon et al. 1974). In our study, we tried to minimize potential effects due to artificial clipping by choosing timing and distribution of clipped branches to match natural deer browsing patterns as closely as possible.

In conclusion, white pine does not appear to fully compensate (sensu Belsky 1986) for lost tissues after simulated browsing. While height growth stimulation occurs, it is limited to conditions when the intensity of simulated herbivory is light and if apical control is broken. Full compensation for lost biomass does not appear to occur in a natural setting, even if competition is precluded from the seedlings. As a result, simulated browsing and any subsequent overcompensation will almost always deplete stored plant reserves, reduce plant vigor, and increase the probability of plant mortality over time (Saunders and Puettmann 1999; Belsky 1986). The variation in compensatory response pattern related to competition from different vegetational components suggests that overcompensation may be an adaptation for competitive ability, rather than a response to herbivory per se (see also Hjältén et al. 1993).

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