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A Retrospective Study of Competition Between Paper Birch and Planted Douglas-fir

by
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SUMMARY

The purpose of this study was to examine the effects of varying amounts of paper birch (*Betula papyrifera* Marsh.) on growth of 7- to 11-year-old Douglas-fir (*Pseudostuga menziesii* var. *glauca* (Mirb.) Franco) in the Interior Cedar-Hemlock (ICH) zone of the southern interior of British Columbia. Competitive interactions in five birch-dominated Douglas-fir plantations were retrospectively examined using a neighborhood approach, where the size of target Douglas-fir was related to the density, size and proximity of neighboring birch. The neighborhood measures were chosen based on the assumption that paper birch affects Douglas-fir growth primarily through competition for light. Two ecological competition thresholds were identified at each site: the first threshold was the birch density at which competition began and Douglas-fir growth was limited; the second was the birch density at which Douglas-fir growth became independent of birch density.

An important limitation to the retrospective approach is that a negative correlation between Douglas-fir size and amount of neighboring birch does not necessarily mean that competition is occurring. Hypotheses can be developed about competitive interactions, but they must be later tested under controlled, replicated and randomized experimental conditions.

Stem diameter and, to a lesser degree, height of Douglas-fir decreased as birch density increased. Consequently, height:diameter ratio increased (i.e., Douglas-fir became more spindly) as birch density increased, a common response among conifers to low light conditions.

The first ecological competition threshold occurred at 0 birch stems per hectare. That is, the largest Douglas-fir were growing free of neighboring birch. As birch density increased, Douglas-fir performance declined sharply, at a rate that was greater on higher than on lower quality sites. The second ecological competition threshold, or the birch density at which Douglas-fir performance did not respond to further increases in birch density, increased from 10 000 to 40 000 birch stems per hectare as site quality decreased. The second threshold occurred at lower birch densities on higher quality sites presumably because the ability of each individual birch to usurp resources from neighboring Douglas-fir was greater. The results suggest that the increase in birch competitive ability as site quality improved was due to greater initial size and faster height growth rates.

The results suggest that birch density must be reduced to below the second ecological competition threshold to improve Douglas-fir growth. Once birch density is below that threshold, additional decreases in density will likely result in substantial increases in Douglas-fir performance. Although the results indicate that maximum Douglas-fir performance will be achieved when all neighboring birch are removed, such treatment is operationally impractical. Retaining a low density of birch at the expense of a small reduction in Douglas-fir growth may have positive effects on site productivity, ecosystem diversity, and the spread of *Armillaria* root rot. A practical alternative to the ecological thresholds is an operational competition threshold — that is, the birch density at which 90% of maximum Douglas-fir performance is achieved. In this study, the operational competition threshold increased from 340 to 2100 birch stems per hectare as site quality decreased.

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1 INTRODUCTION

Douglas-fir (*Pseudostuga menziesii* var. *glauca* (Mirb.) Franco) is an extremely important commercial tree species in the southern interior of British Columbia. It forms extensive stands over much of the southern half of the Interior Plateau. Of all the biogeoclimatic zones in the southern Interior, Douglas-fir reaches its greatest productivity in the Interior Cedar-Hemlock (ICH) zone. On mesic sites, for example, site index at 100 years ranges from 31 to 35 m in the ICH zone compared with only 23 to 29 m in its drier counterpart, the Interior Douglas-fir (IDF) zone (Lloyd *et al.* 1990). Intensive management of Douglas-fir in the highly productive ICH zone may therefore be imperative to meeting future wood demands in the southern interior.

Young Douglas-fir plantations in the ICH zone often perform poorly because of competition with non-crop vegetation. Competitive interactions between Douglas-fir and non-crop vegetation change as species dominance changes over time. For example, competition with herbs and shrubs, such as fireweed (*Epilobium angustifolium*) and thimbleberry (*Rubus parviflorus*), is often responsible for poor survival among recently planted Douglas-fir seedlings. As plantations grow older, intense competition from hardwoods, primarily paper birch (*Betula papyrifera* Marsh.), often result in mortality and poor growth of established Douglas-fir saplings. The competitive effects of birch on Douglas-fir continue to change with time as birch size increases and stand density is regulated through self-thinning. The study focused on the competitive effects of paper birch on established Douglas-fir saplings in 7- to 11-year-old plantations on mesic sites in the ICH zone.

Paper birch is a seral hardwood species which frequently dominates harvested sites in the wetter subzones of the ICH. Its reproductive success on cutover areas can be attributed to rapid and prolific seeding-in to burned or mechanically disturbed areas, and vigorous sprouting from damaged or cut stumps (Haeussler and Coates 1986). The rapid juvenile growth rate of paper birch sprouts (approximately 1 m/yr) gives the species an early competitive advantage over Douglas-fir seedlings. Although no studies have specifically examined competitive interactions between paper birch and Douglas-fir, Gregory (1966) and Arlidge (1967) noted an increased risk of mortality of white spruce under dense birch stands. In addition, several studies have shown reduced Douglas-fir survival and growth when it grows in combination with other hardwood species, specifically red alder (Howard and Newton 1984; Chan and Walstad 1987; Cole and Newton 1987; Chan *et al.* 1988).

Competing birch can hamper Douglas-fir performance by modifying environmental conditions (e.g., temperature) and aggravating resource limitations (e.g., of water, light and nutrient). The effects of competition are seen in the physiological and growth responses of Douglas-fir individuals to the resources and conditions of their microenvironment (Radosevich and Osteryoung 1987). In the ICH zone, where conifer growth is usually not limited by moisture or nutrient availability, competition between Douglas-fir and paper birch appears to be driven primarily by light. Paper birch also impedes Douglas-fir seedling survival and growth by causing physical damage through litterfall, press, and whipping (Haeussler and Coates 1986). In this study, however, the sampling design and methodology were based on the assumption that paper birch affects Douglas-fir saplings primarily through competition for light.

The intent of this study was to investigate, with a neighborhood approach, the competitive interactions between planted Douglas-fir saplings and plant species in paper birch-dominated communities. Through the neighborhood approach, the performance of a target Douglas-fir is related to the species, number, size and aggregation of its neighbors (Mack and Harper 1977; Liddle *et al.* 1982; Weiner 1982, 1984; Goldberg and Werner 1983). The main use of neighborhood analyses is to determine how much variation in the performance of target individuals may be explained by the amount or proximity of neighbors. Several retrospective studies of young established conifer stands have shown that up to 52% of the variation in conifer growth can be accounted for by competitive effects (Weiner 1984; Corns and Pluth 1984; Brand 1986a; Chan and Walstad 1987; Wagner and Radosevich 1987).

Because competitive interactions among species change with site conditions, a range of sites were sampled representing different biogeoclimatic classifications, and therefore different species composition, soils, regional climate and geographical area (Lloyd *et al.* 1990). Competitive interactions were then compared among sites to see if they varied according to site quality.

Studying competition with a retrospective approach has certain limitations which can only be overcome by experimentally creating competition levels (Goldberg and Werner 1983; Wagner and Radosevich 1987). A natural gradient of neighboring species may have an underlying environmental cause which also affects the target species directly. An advantage to retrospective studies, however, is that preliminary models can be developed in a short period of time. These models can provide reasonable hypotheses of competitive effects, which can later be tested under controlled, replicated, and randomized experimental conditions.

2 OBJECTIVES

The objectives of the neighborhood study were:

1. to determine the effects of the species, amount, size and proximity of immediate neighbors on the size of target Douglas-fir saplings on a variety of sites in the ICH zone.
2. to compare competitive interactions among sites so that they may be ranked according to the severity with which neighbors compete with crop trees.

3 METHODS

3.1 Location and Site Description

The five sites selected for this study were located in the ICH zone in the southern interior of British Columbia. Two were located in the ICHmw2 (Shuswap Moist Warm ICH) variant, two in the ICHmw3 (Thompson Moist Warm ICH) variant, and one in the ICHmk1 (Thompson Moist Cool ICH) variant (Lloyd *et al.* 1990). The sites were harvested and planted with Douglas-fir between 1978 and 1981. Currently, the communities are dominated by paper birch and Douglas-fir. Study locations were selected on the basis of species composition, age, hygrotope and biogeoclimatic variant.

Site quality was determined for each location according to the average height of the five tallest Douglas-fir in the stand at a reference age of seven. Table 1 provides a summary of the study site characteristics.

3.2 Sampling Design

Approximately 30 neighborhood plots were sampled within each site during June and July 1989. The neighborhoods were defined by 10-m^2 circular plots centered on healthy, undamaged target Douglas-fir. Plots were chosen to represent a wide range in competitive conditions, from low (0%) to high (100%) paper birch cover. Once a neighborhood of the desired competitive level was located, three to five occupant target Douglas-fir and their neighborhoods were sampled. Within each neighborhood, the performance of the target Douglas-fir was related to the species, amount, aggregation and distance to neighbors.

Sampling was restricted to healthy Douglas-fir to minimize the confounding effects of unknown damaging agents, such as insects, disease, wildlife and abiotic elements. This restriction resulted in a conservative estimate of the negative effects of competition, since Douglas-fir growing under high competitive stress are usually more affected by secondary damage than those under low stress.

3.3 Measurements

Neighborhood plot information that was collected included: size of the target Douglas-fir; species, abundance and proximity of neighbors; and environmental conditions.

TABLE 1. Location, biogeoclimatic classification and site characteristics of study locations

Site No.	Location	Forest District	BEC unit	Ecosystem association[a]	Harvest year	Planting year	Age	Douglas-fir height (m)[b]	Birch height (m)[c]
1	Lee Creek	Salmon Arm	ICHmk1	1 (mesic)	1978	1981	9	1.5	5.8
2	Larch Hills	Salmon Arm	ICHmw2	1 (mesic)	1978	1982	8	1.6	6.4
3	Otter Creek	Clearwater	ICHmw3	1-5 (mesic - subhygric)	1974	1978	11	1.7	7.7
4	Hidden Lake	Vernon	ICHmw2	1 (mesic)	1976	1983	7	1.9	8.3
5	Adams Lake	Clearwater	ICHmw3	1 (mesic)	1979	1982	8	2.2	7.2

[a] Hygrotope is indicated in brackets.
[b] Average height of five tallest measured Douglas-fir at a reference age of seven.
[c] Current average height of five tallest measured paper birch.

Douglas-fir size was quantified as stem diameter (measured at root collar), total height, D^2H ($diameter^2$ x height), and height:diameter ratio.

Neighborhoods were described using both an extensive and a more detailed intensive approach (after Wagner and Radosevich 1987). In the extensive approach, the density and percent cover of paper birch and the percent cover of (1) all shrubs, (2) all herbs, and (3) each of the dominant species were estimated using the quadrant method described by Herring and Pollack (1985). In the intensive approach, each birch in the neighborhood plot was measured separately. Measurements included: height and crown diameter of each birch; and the azimuth and distance from the target Douglas-fir to the middle of each birch crown (Figure 1).

Environmental conditions were partially described for each neighborhood plot; and slope, aspect, organic matter depth, and hygrotope were recorded.

3.4 Analysis

Competition indices were calculated from the extensive and intensive neighborhood measures. The indices quantified the amount of interference a target tree experienced from neighboring vegetation. Extensive indices (Table 2) were equivalent to the density and percent cover of birch and percent cover of the other dominant competing species in the plot.

The intensive indices were the sums of individual vegetation measures from all birch individuals in the plot (e.g., sum of heights). To make the indices distance-dependent, the height, crown area or crown volume was divided by the distance of each birch individual in the plot from the target Douglas-fir. Azimuth values for each birch were used to calculate angular dispersion (Zar 1974; Mack and Harper 1977; Wagner and Radosevich 1987). Angular dispersion, an index of the arrangement of birch around each target Douglas-fir, ranged from zero to one. A value of zero indicated that the birch were clumped at one azimuth from the tree; a value of one indicated that all birch were evenly distributed around the tree. The intensive indices developed are presented in Table 3.

A crown competition factor (CCF) and height-spacing index (HSI) were also evaluated (after Daniel *et al.* 1979). The CCF was used to estimate the degree of crowding among birch stems. First, the maximum density of birch trees that grew on a specified area without experiencing intraspecific competition was estimated for each site according to the crown area of the largest open-grown tree. Second, the CCF was calculated as the ratio of plot density to the maximum density. If the CCF was greater than 1, then each birch tree on the plot had less space than it would occupy when open-grown. If the CCF was less than 1, then it was assumed the birch trees were not fully using the space available. The HSI accounts for both the size and degree of crowding of birch stems. The height of the dominant birch was divided by the average inter-tree spacing for each plot.

TABLE 2. Extensive competition indices that were evaluated in the study

Index	Description
1	Percent cover of all hardwoods
2	Percent cover of all shrubs
3	Percent cover of all herbs
4	Percent cover of paper birch
5	Density of paper birch
6	Percent cover of thimbleberry
7	Percent cover of falsebox

TABLE 3. Intensive competition indices that were evaluated in the study

Symbol	Description
Indices using 1 vegetation parameter[a]	
CAS	sum of CA
HEIGHTS	sum of HT
DISTS	sum of D
IDS	sum of inverse of D ID = 1/D
ID2S	sum of inverse of the square of D ID2 = $1/D^2$
ANGDIS	angular dispersion = $\sqrt{\frac{1 - (\cos(z_i)^2 + \sin(z_i)^2)}{n}}$
Indices using 2 vegetation parameters	
ADHS	ANGDIS * (sum of HT)
CHS	sum of CA*HT
CDS	sum of CA/D
HDS	sum of HT/D
CD2S	sum of CA/D^2
HD2S	sum of HT/D^2
ADDS	ANGDIS * (sum of D)
ADD2S	ANGDIS * (sum of D^2)
ADNUM	ANGDIS * density of birch
HNUM	(sum of HT) * density of birch
DNUM	(sum of D) * density of birch
Indices using 3 vegetation parameters	
CHDS	sum of (CA * HT)/D
CHD2S	sum of (CA * HT)/D^2
ADCHS	ANGDIS * sum of (CA * HT)
ADHD2S	ANGDIS * sum of (HT/D^2)
Indices using 4 vegetation parameters	
ADCHDS	ANGDIS * (sum of (CA * HT)/D)
ADCHD2S	ANGDIS * (sum of (CA * HT)/D^2)

[a] HT = height (cm) of birch individuals within the plot.
D = distance (cm) from target Douglas-fir stem to the nearest crown edge of birch individuals within the plot.
CA = 3.1416*(crown diameter of birch individuals/2)^2.
z_i = azimuth from the target tree to the center of birch individual i.
n = number of individual birches within the plot.

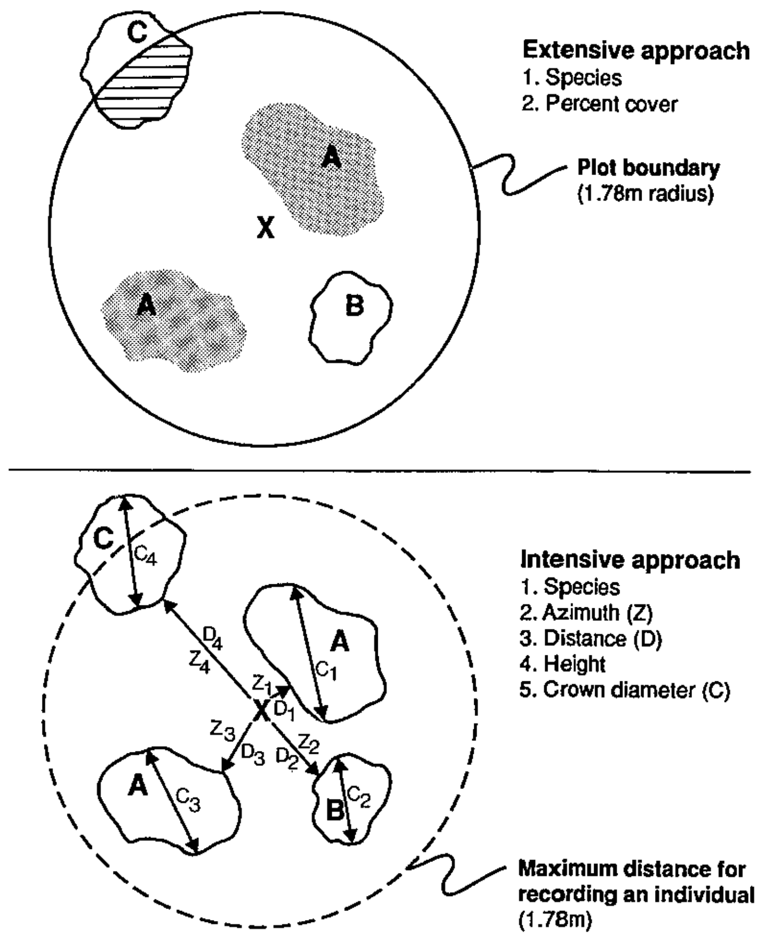

FIGURE 1. Vegetation parameters measured by the (a) extensive and (b) intensive approaches to quantifying interspecific competition (after Wagner and Radosevich 1987).

Multiple regression models were constructed relating Douglas-fir performance (dependent variable) to the competition indices, CCF and HSI (independent variables) for the most responsive performance variables. The relationships were evaluated and the "best" models were chosen according to the combination of indices that had the highest R^2 values and included the fewest number of independent variables. Regression coefficients, measures of the competitive effects of paper birch on Douglas-fir, were compared statistically among sites.

Two ecological and one operational competition thresholds were identified at each site based on individual Douglas-fir growth (Figure 2). The first ecological threshold was the birch density, or number of neighbors, at which competition began and Douglas-fir growth was limited (Cussans *et al.* 1986). An increase in density over the first threshold point resulted in a sharp decrease in yield until a second ecological threshold was reached. The second ecological threshold was the point at which Douglas-fir growth became independent of birch density, i.e., the curve flattened out (Goldberg and Werner 1983). That is, the second ecological threshold occurred where Douglas-fir growth was so suppressed by surrounding birch that additional increases in birch density resulted in no further reductions in Douglas-fir growth.

Ecological thresholds are sometimes operationally impractical to achieve. To reach an ecological threshold of 0 birch stems per hectare, for example, would be very expensive and require annual re-treatment. Conversely, retaining a low density of birch at the expense of a small reduction in Douglas-fir growth might have positive effects on soil nutrient capital, spread of *Armillaria* among Douglas-fir, and ecosystem diversity. An operational competition threshold was thus defined as the birch density at which 90% of the maximum Douglas-fir size (i.e., size at the first ecological competition threshold) is attained.

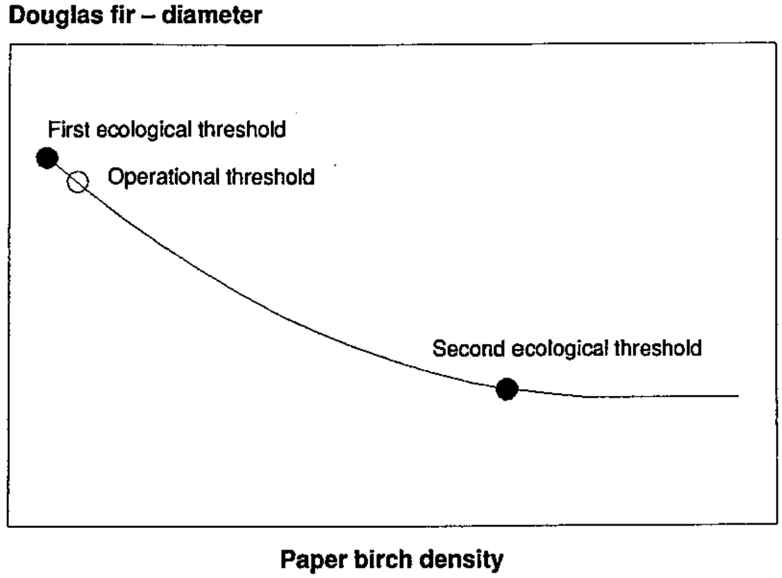

FIGURE 2. Ecological and operational competition thresholds.

Thresholds were compared among sites to determine whether or not they differed according to site quality.

4 RESULTS AND DISCUSSION

4.1 Site Quality

Site index is the most common method of quantitatively determining site quality. Site index curves, however, are of limited reliability below the age of 20 years (B.C. Ministry of Forests 1986). In this study, we determined site quality by comparing the average height of the five tallest Douglas-fir at a reference age of seven, among the five sites (Figure 3).

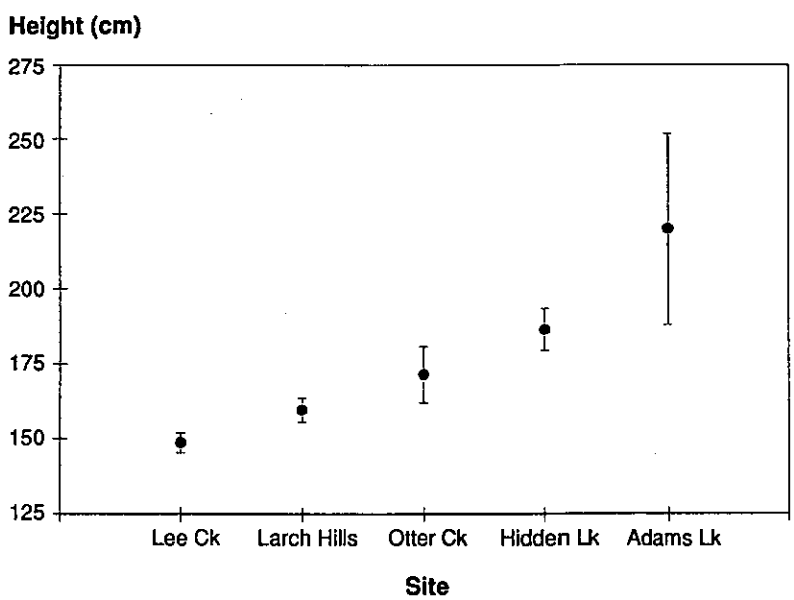

FIGURE 3. Mean height of five tallest Douglas-fir at a reference age of seven on the five sites sampled.

Sites were ranked according to site quality (Table 1). With one exception, sites in the ICHmw3 (Thompson Moist Warm ICH) variant were of better quality than those in the ICHmw2 (Shuswap Moist Warm ICH) and ICHmk1 (Thompson Moist Cool ICH) variants. The better Douglas-fir height growth on the ICHmw3 sites over that in the ICHmw2 and ICHmk1 sites is consistent with the average site index values reported by Lloyd *et al.* (1990).

4.2 Neighborhood Analyses of Individual Sites

Of all the Douglas-fir size variables evaluated, stem diameter and height:diameter ratio were best related to competition indices. Stem diameter and, to a lesser degree, height decreased as the amount of neighboring vegetation increased. Consequently, height:diameter ratio increased (i.e., Douglas-fir became more spindly) as the amount of neighboring vegetation increased. The relative sensitivity of diameter compared to height growth under competitive stress has been commonly observed in young plantations when seedlings become spindly as a result of reduced light under overtopping vegetation (Lanner 1985; Brand 1986a; Cole and Newton 1987; Wagner and Radosevich 1987; Zedaker *et al.* 1987).

Height:diameter ratio is a measure of the relative allocation of resources, particularly carbon, to cambium and height growth. Lanner (1985) suggests that when seedlings are under stress, the strongest sink for carbohydrates, next to developing cones, is elongating shoots. Elongating shoots draw on stored carbohydrates early in the season, while cambium depends more on current photosynthate, and so is more influenced by resource limitations resulting from competition with birch. Under competition stress, Douglas-fir shoots are not only a higher priority than active cambium, but they are closer to the sources of photosynthate, the needles. Furthermore, trees growing under high competitive stress have small crowns and therefore need less stem tissue for support. Increased height growth under greater competition is also advantageous to Douglas-fir because more of its foliage is exposed to sunlight. Changes in the relationship of height to diameter have been related by some researchers to reductions in solar radiation availability as a result of interference from overtopping vegetation (Brix 1970; Howard and Newton 1984; Pearson *et al.* 1984; Brand 1986b).

4.2.1 Extensive competition indices

Percent cover

Percent cover of birch was the extensive competition index best related to Douglas-fir size on all sites. As the percent cover of neighboring birch increased, Douglas-fir diameter decreased (Figure 4). A linear model best described the relationship between Douglas-fir stem diameter and birch cover; logarithmic transformations of Douglas-fir diameter marginally helped correct for non-linearity for only three sites. In western Oregon, estimates of percent cover of neighboring vegetation have also been valuable for predicting seedling growth in Douglas-fir plantations (Wagner and Radosevich 1987). In this study, between 25 and 79% of the variation in Douglas-fir diameter was explained by birch cover on the five sites studied (Table 4). The amount of variation accounted for by birch was within the range reported in other retrospective studies of interspecific competition in conifer stands (Corns and Pluth 1984; Weiner 1984; Brand 1986a; Wagner and Radosevich 1987).

The competitive effect of a neighbor species on a target species can be ascertained from the slope of the regression of the size (e.g., diameter) of the target Douglas-fir on the amount (e.g., percent cover or density) of neighbors (Goldberg and Werner 1983). Since the slope has a variance associated with it, the competitive effect of several neighbor species can be compared statistically and ranked in terms of the magnitude of the species' competitive effects on target Douglas-fir. In this study, paper birch had a more negative effect on Douglas-fir than did any of the other neighboring species. Paper birch cover explained more variation in Douglas-fir size than did any of the other extensive indices tested. It was also the most abundant and one of the largest species in the community. Goldberg and Werner (1983) suggest, per unit, competitive effects are similar among individual species since they all require the same resources (light, water and nutrients). Differences in per-unit competitive effects that do exist, they add, are often overshadowed by size differences between individual neighbors. Clearly then, larger plants, such as paper birch, are likely to have a greater effect than smaller plants, such as fireweed and thimbleberry, simply because they can take up more resources (Harper 1977).

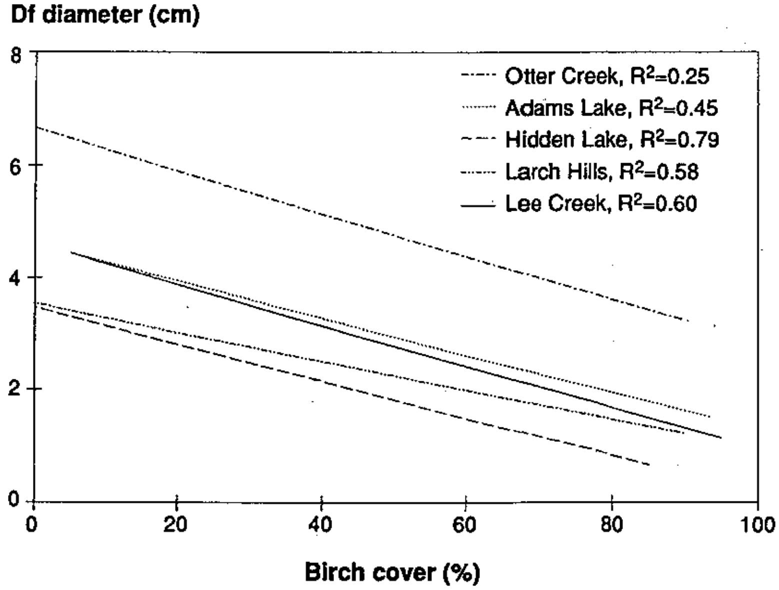

FIGURE 4. Relationship between Douglas-fir stem diameter and paper birch cover on the five sites sampled.

The competitive effects of paper birch on Douglas-fir were not significantly different among sites (p=0.05). However, differences owing to plantation age, and hence to Douglas-fir diameter, did show up. The amount of variation in Douglas-fir diameter explained by birch cover was considerably lower at the Otter Creek site than at the other four. Birch[1] made up 59% and conifers (predominantly western redcedar and western hemlock) 41% of the stand at Otter Creek. In contrast, birch made up between 85 and 96% and conifers (a mixture of Douglas-fir, western redcedar, western hemlock, western white pine, Engelmann spruce and/or western larch) only between 4 and 15% of the stand at the other four sites. The high component of conifers at Otter Creek likely had a significant effect on Douglas-fir performance, which was not accounted for in the regression models. In general, as the conifer component increased among sites, the amount of variation in Douglas-fir performance accounted for by birch cover decreased.

Density

Douglas-fir size decreased as paper birch density increased (Figure 5). Quadratic regression models of birch density were only slightly less predictive than percent cover for Douglas-fir stem diameter or height:diameter ratio on all sites (Table 5). Although there is no apparent reason why, stem diameter was the more responsive size measure at Hidden Lake, Lee Creek and Otter Creek, and height:diameter ratio at Adams Lake and Larch Hills. The relationship between Douglas-fir size and birch density is consistent with yield-density theory, where the effect of density on individual plant yield is described by either a negative exponential (Kira *et al.* 1953; Harper 1977) or negative hyperbolic function (Weiner 1984).

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[1] Includes paper birch and minor components of trembling aspen (*Populus tremuloides*) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*).

TABLE 4. Linear regression models relating Douglas-fir stem diameter to the extensive index, birch cover, for 10-m^2 plots within each of the five study sites. The general form of the model was: y = a + bx, where y=Douglas-fir stem diameter and x=birch cover.

Variable	Site Adams Lk	Otter Ck	Hidden Lk	Larch Hills	Lee Ck
Stem diameter					
Intercept	4.503b[1]	6.658a	3.470c	3.545c	4.433b
Slope (birch cover)	-0.029a[2]	-0.038a	-0.033a	-0.026a	-0.032a
Model R^2	0.45	0.25	0.79	0.58	0.60
p-value	0.0001	0.0029	0.0001	0.0001	0.0001
n	30	36	31	31	24

1 Intercepts with different letters are different at the 0.05 significance level.
2 Slopes with different letters are different at the 0.05 significance level.

TABLE 5. Quadratic regression models relating stem diameter and height:diameter ratio to the extensive index, birch density, for 10-m^2 plots within each of the five study sites. The general form of the model was: $y = a + bx + cx^2$, where y=Douglas-fir stem diameter or height:diameter ratio and x=birch density. All intercepts and slopes were different among sites at the 0.05 significance level.

Variable	Site Adams Lk	Otter Ck	Hidden Lk	Larch Hills	Lee Ck
Stem diameter					
Intercept	4.189	7.526	3.338	3.505	4.098
Birch density	-0.168	-1.223	-0.287	-0.096	-0.062
Birch density^2	0.004	0.097	0.009	0.001	0.0003
Model R^2	0.24	0.34	0.71	0.48	0.39
p-value	0.0228	0.0183	0.0001	0.0001	0.0058
n	30	36	31	31	24
Height:diameter ratio					
Intercept	38.848	41.304	51.430	47.577	39.552
Birch density	2.787	4.824	2.134	1.115	1.607
Birch density^2	-0.047	-0.320	-0.053	-0.011	-0.020
Model R^2	0.69	0.31	0.39	0.60	0.37
p-value	0.0001	0.0276	0.0011	0.0001	0.0077
n	30	36	31	31	24

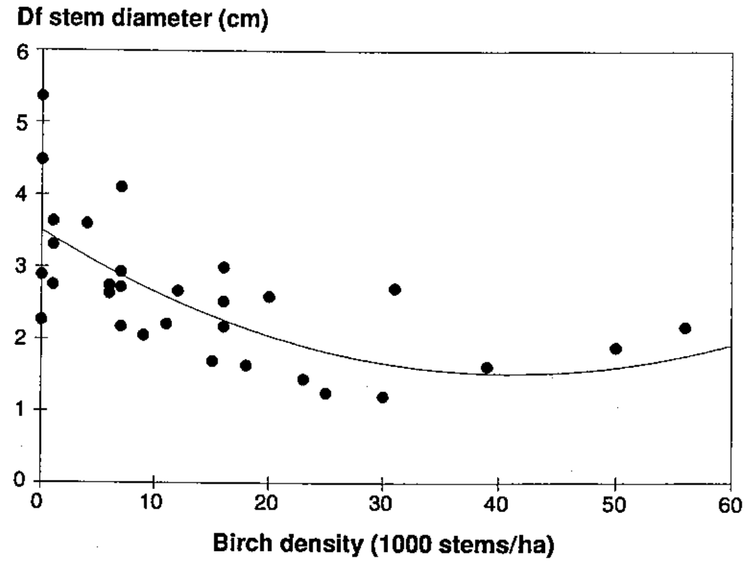

FIGURE 5. Relationship between Douglas-fir stem diameter and paper birch density at Larch Hills.

Ecological competition thresholds were identified by the shape of the curves relating Douglas-fir stem diameter and height:diameter ratio to birch density on each of the sites (Figures 6 and 7). The first ecological threshold — that is the density of birch at which competition began and Douglas-fir growth was limited — was 0 stems per hectare on all sites. In other words, the best Douglas-fir performance occurred in the absence of neighboring birch. As density increased, Douglas-fir performance declined sharply. The rate of decline varied significantly among all sites ($p=0.05$); and in general, was greater on higher than lower quality sites. That is, the competitive effect of paper birch, as estimated by the first-order regression coefficient of birch *density* on Douglas-fir size, appeared to increase with site quality (Table 5).

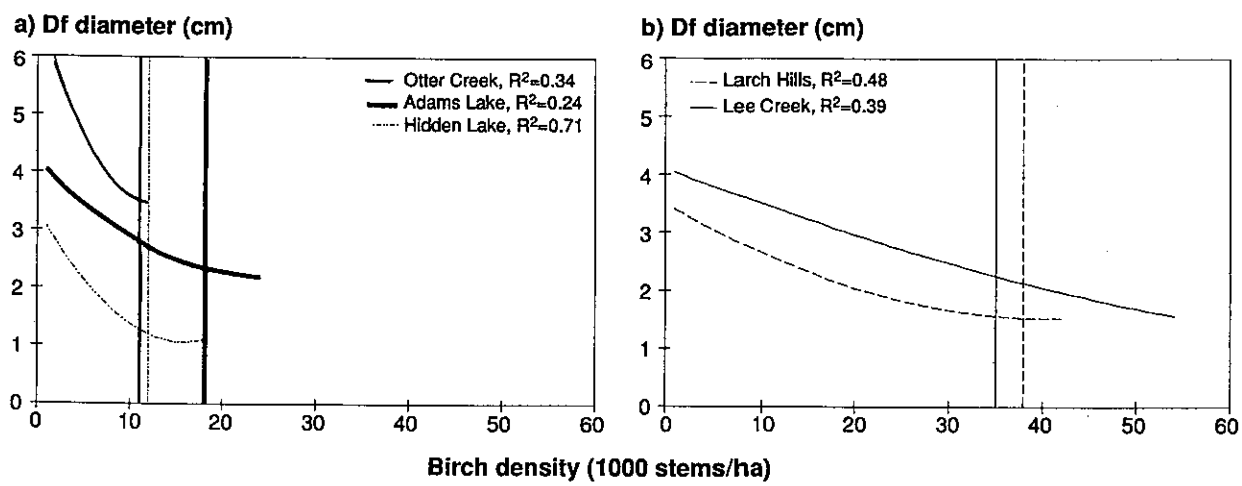

FIGURE 6. Relationship between Douglas-fir stem diameter and paper birch density on the five sites sampled. The first ecological threshold is at 0 stem/ha on all sites and the second ecological thresholds are indicated by the vertical lines.

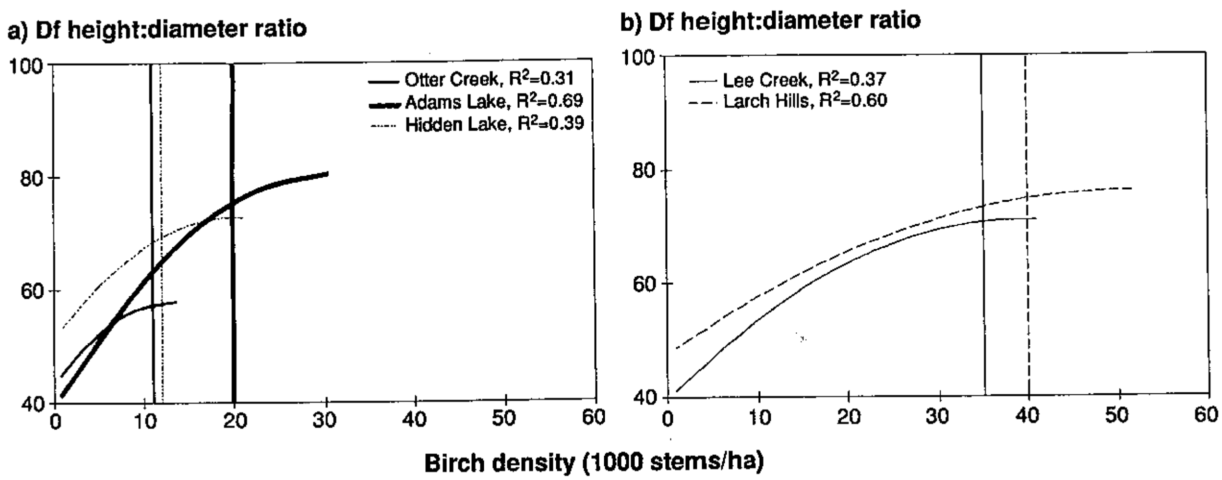

FIGURE 7. Relationship between Douglas-fir height:diameter ratio and paper birch density on the five sites sampled. The first ecological threshold is at 0 stems/ha and the second ecological thresholds are indicated by the vertical lines.

The second ecological threshold — the birch density at which Douglas-fir did not respond to further increases in birch density — also varied according to site quality. It increased from 10 000 to 40 000 stems per hectare as site quality and birch height decreased (Figure 8). The second threshold occurred at lower birch densities on higher quality sites because the ability of each individual birch to usurp resources, primarily light, from neighboring Douglas-fir increased. The increase in birch competitive ability with site quality was presumably a result of increased resource availability, greater initial plant size, and different resource use patterns.

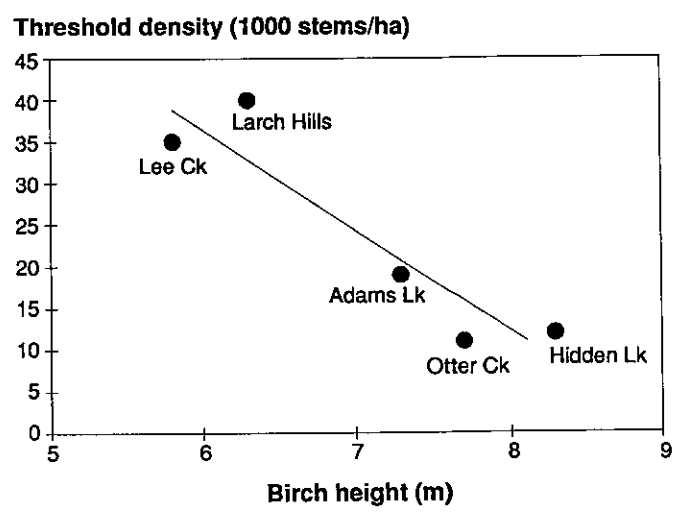

FIGURE 8. Relationship between birch density at the second ecological threshold and dominant birch height on the five sites sampled.

The principles underlying competitive interactions in single-species stands can be applied to mixed stands of paper birch and Douglas-fir (Radosevich and Holt 1984). In pure birch stands, competition regulates the relationship between size and density through self-thinning. At low density, or during the initial phase of growth, yield is determined by the number of individuals. At high densities, or as plants grow larger, yield is determined by the resource-supplying power of the environment (law of constant final yield). Total yield may be determined by many small birches or, because of self-thinning, by fewer larger ones. Increasing resource availability, from low to high quality sites, for example, results in an increase in total yield but does not necessarily alter the relationship between yield and density. Greater resource availability on high rather than low quality sites, however, enhances self-thinning among birch. This happens because the dominant trees continue to capture most of the resources and, consequently, the larger trees become more dominant while the smaller ones become more suppressed or die. The number of birch trees therefore actually decreases while total yield increases with site quality.

In mixed paper birch/Douglas-fir stands there also is a premium on early establishment and growth of birch seedlings. When Douglas-fir seedlings are planted, they are at a competitive disadvantage because birch seedlings are already established and rapidly growing. With increasing site quality, this disadvantage increases for two reasons. First, birch seedlings grow at a faster rate and thus are initially larger on better than poorer sites. Second, because of the ecological differences between the two species, birch is better able than Douglas-fir to use increased resources for height growth. The results indicate that not only does total yield of mixed stands increase with site quality, but the relative proportion of birch to Douglas-fir increases as well.

Differences in the competitive effect of birch on Douglas-fir were evident among sites when birch amount was measured as density, but not as percent cover. Presumably, a given percent cover of birch intercepts the same amount of light regardless of the site on which it was measured. As site quality increased and birch size increased, however, the ability of each individual birch to intercept light increased. Fewer birch were required to compete for the same amount of light. Indeed, birch density was lower and the competitive effect greater as site quality increased.

Management practices must aim at reducing birch density at least to below the second ecological competition threshold; otherwise, Douglas-fir growth increases will not be realized. Once density is below that threshold, any additional decrease will result in a substantial and predictable increase in Douglas-fir performance. The results indicate that maximum Douglas-fir performance will be achieved only when all birch is removed. Operationally, such treatment is very difficult, if not impossible. A practical alternative is to set an operational competition threshold, or the birch density at which 90% of maximum Douglas-fir size can be achieved. The operational threshold in this study ranged from 340 stems per hectare at Otter Creek to approximately 2100 stems per hectare at Larch Hills (Figure 9).

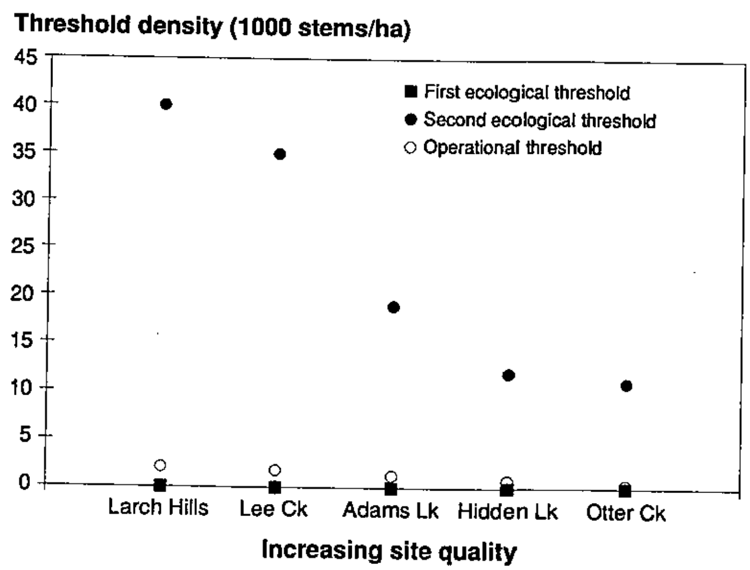

FIGURE 9. Comparison of competition thresholds among the five study sites.

Crown competition factor and height/spacing index

The CCF and, to a greater degree, HSI were well related to Douglas-fir size on all sites sampled (Appendix 1). As with the birch density relationship, Douglas-fir stem diameter was best related to CCF on some sites and to height:diameter ratio on others. As birch crowding (CCF) increased, Douglas-fir stem diameter decreased and height:diameter ratio increased. Similarly, as birch height increased and inter-tree spacing decreased (i.e., HSI increased), Douglas-fir performance decreased. Although quadratic transformations of CCF and HSI slightly improved the fit of the regression models, ecological competition thresholds could not be easily identified from the curves generated.

4.2.2 Intensive competition indices

Intensive indices did not explain any more variation in Douglas-fir performance than did the extensive indices on all sites sampled. The best intensive index for all sites, HDS (height/distance), explained between 38 and 76% of the variation in Douglas-fir diameter and height:diameter ratio (Table 6).

TABLE 6. Regression models relating Douglas-fir size to the intensive competition index, HDS, for 10-m^2 plots within each of the five study sites. The general form of the model was $y = a + bx$, where y=Douglas-fir size and x=HDS.

	Site				
Variable	**Adams Lk**	**Otter Ck**	**Hidden Lk**	**Larch Hills**	**Lee Ck**
Dependant variable	Height: diameter ratio	Inverse diameter	Diameter	Height: diameter ratio	Diameter
Intercept	45.189	0.135	3.000	50.208	4.054
HDS	0.349	0.005	-0.018	0.227	-0.014
Model R^2	0.76	0.41	0.51	0.57	0.49
p-value	0.0001	0.0013	0.0001	0.0001	0.0002
n	30	36	31	31	24

The intensive indices tested in regression models could help explain the processes by which paper birch competes with Douglas-fir saplings. For example, height, distance to target Douglas-fir, and angular dispersion of surrounding birch affect how much light is available to target Douglas-fir (Mack and Harper 1977; Weiner 1984). The single, most predictive intensive index was HDS, suggesting that paper birch is limiting Douglas-fir growth by reducing light availability.

5 SUMMARY AND RECOMMENDATIONS

The intent of this study was to investigate competitive interactions between Douglas-fir and paper birch saplings in the Interior Cedar Hemlock zone in the southern interior of British Columbia. Competitive interactions were retrospectively examined among 7- to 11-year-old planted Douglas-fir and paper birch on five sites in a neighborhood approach. With that approach, we related the performance of Douglas-fir individuals to the species, number, size, and aggregation of its neighbors (Mack and Harper 1977; Liddle *et al.* 1982; Weiner 1982,1984; Goldberg and Werner 1983). Studying competition with a retrospective approach is limited because there may be an underlying environmental cause which affects both Douglas-fir and paper birch. Although the results demonstrate the existence of a correlation between Douglas-fir size and paper birch density, they do not necessarily mean causation.

The results suggest that on all sites sampled, paper birch had a greater competitive effect on Douglas-fir than did the other dominant species in the community. Paper birch, however, was also the largest neighbor and of nearest size symmetry to Douglas-fir. The size difference between paper birch and the other neighbors likely overshadowed species differences in resource use patterns.

Birch density was of value for predicting Douglas-fir diameter and height:diameter ratio on all sites. The quadratic relationships between birch density and Douglas-fir size facilitated the identification of ecological competition thresholds. The first ecological threshold (the birch density at which competition began and Douglas-fir growth was limited) was 0 stems per hectare on all sites. The second ecological threshold (the point at which Douglas-fir growth became independent of paper birch density) increased from 10 000 to 40 000 stems per hectare as site quality decreased. At that threshold, Douglas-fir were so suppressed by surrounding birch that additional increases in birch density resulted in no further reductions in Douglas-fir growth. These findings suggest that, for any given density, paper birch had a greater competitive effect on Douglas-fir on higher quality sites because (a) the second ecological threshold occurred at much lower birch densities, and (b) the rate at which Douglas-fir size decreased as birch density increased was more rapid. As site quality increased, better environmental conditions and greater resource availability resulted in more rapid growth of birch, and hence a greater ability for it to usurp resources from neighboring Douglas-fir.

Birch percent cover, unlike density, did not indicate differences in competitive effects among sites. A given percent cover of birch presumably intercepts the same amount of light regardless of the site on which it is measured. However, as site quality and birch size increased, the ability of each birch to intercept light also increased. Consequently, fewer birch were required to compete for the same amount of light as site quality increased. Indeed, birch density was lower and the competitive effect greater as site quality increased.

The single intensive index which best predicted Douglas-fir size was the sum of birch heights, divided by distance to the target Douglas-fir (HDS). According to Weiner (1984), the measures, height and distance, suggest that light availability is being limited by neighboring birch. In other words, relative to competition for moisture and nutrients, light may be more important in driving competitive interactions in these communities.

Our study also indicated that the potential size of a Douglas-fir in the ICH zone was partially a function of its age and competitive environment. A considerable amount of variation in Douglas-fir size, however, remained unexplained. ***The regression models, therefore, should not be used as predictors of Douglas-fir growth, but rather as means for identifying factors which may be important to performance.*** Once the important factors limiting Douglas-fir growth are identified, prescriptions can be developed which use appropriate methods for improving the seedling's environment.

The preliminary models developed in this study suggest that ecological competition thresholds *do* exist in Douglas-fir-paper birch communities, and that the thresholds vary with site quality. The models also suggest that paper birch competes with Douglas-fir primarily for light. These hypotheses need to be tested under controlled, replicated, and randomized experimental conditions before site-specific guidelines for vegetation management can be made. In the interim, however, the following recommendations can be made:

1. *In 7- to 11-year-old, mesic, paper birch-dominated Douglas-fir plantations*, vegetation management efforts should focus on birch reduction, since birch appears to be the strongest competitor with Douglas-fir. Other hardwoods, such as trembling aspen and black cottonwood, which form a minor component of the community, likely have a similar competitive effect to birch since they are of similar size and growth form. When Douglas-fir are 1-3 m tall, little effort need

be concentrated on the control of herbs and low-growing shrubs, since those plants appear to have a minor effect on Douglas-fir size.

This recommendation applies only to the specified stage of development because competitive interactions are dynamic, changing with the age of the community. During Douglas-fir seedling establishment, for example, herbs and low-growing shrubs are likely more competitive with Douglas-fir than paper birch seedlings because they are more abundant. Birch becomes important as a competitor when it encroaches, overtops and shades Douglas-fir seedlings. Its competitive effects continue to change with time as its size increases and stand density is regulated through self-thinning.

2. *In 7- to 11-year-old, mesic, paper birch-dominated Douglas-fir plantations,* birch density apparently must be reduced to below 10 000-20 000 stems per hectare on higher quality sites and 35 000–40 000 stems per hectare on poorer sites if improvements in growth are to occur. Additional decreases in density should result in substantial and predictable increases in Douglas-fir performance. The results indicate that best performance will be achieved when all birch is removed.

   Although complete removal of neighboring birch results in the greatest Douglas-fir growth, such a treatment is operationally very difficult to achieve. However, retaining of a low density of birch at the expense of a small reduction in Douglas-fir growth may have positive effects on soil nutrient capital, spread of *Armillaria* among Douglas-fir, and ecosystem diversity. Mixed stands of Douglas-fir and paper birch are gaining favor economically as well, as the market value of paper birch increases in the southern interior. Consequently, an operational competition threshold is suggested to be the birch density at which 90% of maximum Douglas-fir size can be achieved. On high quality sites this was approximately 340 stems per hectare, and on medium quality sites approximately 2100 stems per hectare.

3. Carefully controlled, replicated and randomized competition experiments should be initiated, in which Douglas-fir and paper birch are grown in a mixture at varying densities and proportions. Such experiments would improve the accuracy of the ecological thresholds identified, and provide information on each species' (a) physiological responses to competition, and (b) effects on site productivity, soil development, and ecosystem diversity.

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APPENDIX 1. Linear regression models relating Douglas-fir size to CCF and HSI

TABLE I. Linear regression models relating stem diameter and height:diameter ratio to crown competition factor (CCF) for 10-m^2 plots within each of the five study sites. The general form of the model was: y = a + bx , where y=Douglas-fir stem diameter or height:diameter ratio and x=CCF.

	Site				
Variable	**Adams Lk**	**Otter Ck**	**Hidden Lk**	**Larch Hills**	**Lee Ck**
Stem diameter					
Intercept	3.597	6.425	2.838	3.093	3.093
CCF	-0.001	-0.004	-0.001	-0.001	-0.002
Model R^2	0.14	0.21	0.45	0.32	0.38
p-value	0.0402	0.0304	0.0001	0.0009	0.0012
n	30	36	31	31	24
Height:diameter ratio					
Intercept	46.692	44.928	54.339	51.451	48.247
CCF	0.025	0.023	0.014	0.018	0.016
Model R^2	0.59	0.26	0.33	0.51	0.27
p-value	0.0001	0.0017	0.0001	0.0001	0.0001
n	30	36	31	31	24

TABLE II. Linear regression models relating stem diameter and height:diameter ratio to the height/spacing index (HSI) for 10-m^2 plots within each of the five study sites. The general form of the model was: y = a + bx , where y=Douglas-fir stem diameter or height:diameter ratio and x=HSI.

	Site				
Variable	**Adams Lk**	**Otter Ck**	**Hidden Lk**	**Larch Hills**	**Lee Ck**
Stem diameter					
Intercept	4.145	6.924	3.364	3.485	4.532
HSI	-0.205	-0.563	-0.234	-0.179	-0.253
Model R^2	0.30	0.28	0.71	0.46	0.44
p-value	0.0016	0.0117	0.0001	0.0001	0.0004
n	30	36	31	31	24
Height:diameter ratio					
Intercept	38.154	41.294	49.954	46.074	41.894
HSI	4.306	3.433	2.275	2.714	2.806
Model R^2	0.78	0.40	0.42	0.63	0.32
p-value	0.0001	0.0015	0.0001	0.0001	0.0037
n	30	36	31	31	24