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Conifer–*Ceanothus* interactions influence tree growth before and after shrub removal in a forest plantation in the western Cascade Mountains, USA

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Abstract

Ceanothus velutinous is often considered to be an aggressive competitor with young conifers in the western United States. Using a conifer (noble fir, Pacific silver fir, Douglas-fir, and western hemlock) plantation in western WA where *Ceanothus* had become established, we assessed how conifer–shrub crown interactions affected individual tree growth before and after cutting *Ceanothus* from around individual trees. For all conifer species, trees surrounded by but with leaders above *Ceanothus* were 18–70% taller than open-grown trees, and trees with leaders below *Ceanothus* were 22–50% shorter than open-grown trees; suggesting that *Ceanothus* had both positive and negative effects on tree growth. Few seedlings (8%) of Douglas-fir were found under *Ceanothus*. However, because of shade-intolerance, Douglas-fir growing under *Ceanothus* exhibited the greatest reduction in height (53%) compared to open-grown trees. The most shade-tolerant species, Pacific silver fir, had the least reduction in height (22%) under *Ceanothus*, yet because of its slow growth, most of its seedlings (62%) were found growing under *Ceanothus*. Twelve years after cutting *Ceanothus*, growth rates increased for all four tree species independent of the type of previous interaction with *Ceanothus*; however, mean tree heights and diameters for all four conifers remained substantially lower for trees that had been overtopped by *Ceanothus* compared to trees with leaders not overtopped at the time of release. Thus, the benefits of growing with or being released from encroachment by *Ceanothus* will vary with conifer species and the degree of conifer–shrub interaction and may persist for many years.

Keywords: Conifer growth; Shrub competition; *Ceanothus*; Noble fir; Pacific silver fir; Douglas-fir; Western hemlock

1. Introduction

Growth of young conifers in naturally regenerated or planted forest stands is often slowed by competition with shrubs or herbaceous species (Zavitkovski et al., 1969; Conard and Radosevich, 1982; Conard, 1985; Petersen et al., 1988; Lopushinsky and Klock, 1990; White and Newton, 1990; Monleon et al., 1999; Rose and Ketchum, 2002). *Ceanothus velutinous* Dougl. *var. laevigatus* (snowbrush or varnishleaf) is considered a particularly aggressive competitor with young conifers in much of the west. *Ceanothus* seeds can remain viable for several centuries and will germinate after fire (Conard, 1985). Within a decade after wildfire or prescribed burning following harvesting, *Ceanothus* may reach 2 m in height (Zavitkovski, 1966), forming dense stands that potentially overtop young conifers. Conifer growth reduction by *Ceanothus* has been attributed to competition for light (Conard, 1985), soil moisture (Conard and Radosevich, 1982; Petersen et al., 1988), and nutrients (Powers and Reynolds, 1999).

Ceanothus can also have positive effects on conifer growth (Youngberg, 1966; Scott, 1970; Horowitz, 1982). Seedlings may benefit from the cooler temperatures (Youngberg, 1966; Scott, 1970; Jones, 1995) and increased surface soil moisture (Scott, 1970) under *Ceanothus*. Shading may protect against winter desiccation and excessive radiation loading (Conard and Radosevich, 1982), especially on exposed southerly slopes. *Ceanothus* may also benefit conifer growth by providing physical protection against browse damage (Scott, 1970). In

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addition, *Ceanothus* symbiotically fixes atmospheric nitrogen (N) (Binkley et al., 1982; McNabb and Cromack, 1983; Busse, 2000), which can lead to high pools of total soil N (Youngberg, 1966; Scott, 1970; Johnson, 1995; Spears et al., 2001), favorable soil C:N ratios (Powers and Reynolds, 1999), and high soil N availability (Binkley et al., 1982; Spears et al., 2001).

Many field studies examining *Ceanothus*–conifer competition are conducted at the stand scale and use mean percent cover or stem density to indicate potential competition by *Ceanothus* (e.g., Monleon et al., 1999; Powers and Reynolds, 1999). However, shrub cover is often extremely variable within a stand; crowns of individual trees can range from being free from shading to being completely overtopped by a neighboring shrub. In addition, there can be a range in shrub cover associated with each level of overtopping. Scott (1970) and Horowitz (1982) found that conifers growing at the edges of *Ceanothus* had greater height growth compared with conifers growing either completely under *Ceanothus* or out in the open, suggesting that some degree of interaction with *Ceanothus* may be beneficial for conifer growth. A better understanding of how interactions between individual tree and *Ceanothus* canopies influence tree growth could help managers decide when conditions in a stand might warrant modification.

Despite the potential benefits of *Ceanothus* on conifer growth, *Ceanothus* is often treated with herbicide or manually cut in newly established stands because of the well-documented negative effects of shrub competition on growth. Conifer growth responses to removal of *Ceanothus* vary substantially. Height and diameter growth increased relative to un-released trees in some studies (Gratkowski and Lauterbach, 1974; Petersen et al., 1988; Powers and Reynolds, 1999); however, growth reductions have also been reported (Petersen, 1980; Conard and Radosevich, 1982), especially if release increases stress from solar loading. Post-release conifer growth can also be influenced by a tree's crown position relative to *Ceanothus* (Gratkowski and Lauterbach, 1974; Horowitz, 1982), again suggesting that studies at the individual tree scale may help explain the variation in post-release growth responses.

Our goal was to resolve several questions that might be answered best with detailed information on individual tree–shrub crown interactions: Is the growth of a tree influenced by how much of its crown is covered by a neighboring *Ceanothus*? Do some conifer–*Ceanothus* crown interactions positively influence tree growth? Does tree growth after release depend on a conifer's tolerance to shade or on its crown position relative to *Ceanothus* before release?

We addressed these questions in an experimental conifer plantation at the Wind River experimental forest in the western Washington Cascades where *Ceanothus* had naturally encroached. The plantation was designed to monitor height and diameter growth of several conifer species planted as monocultures or dual-species mixtures. Ten years after planting, *Ceanothus* had become a significant component of the stand (percent canopy cover of *Ceanothus* ranged from 15 to 85%). At this time it was decided to manually clear the *Ceanothus* from around the base of individual trees; we refer to this activity as "release" as it was the intent of the operation to release the planted conifers from current or potential future overtopping. Prior to removal, the amount of crown interaction between *Ceanothus* and individual trees was visually estimated and tree heights were measured. Responses in growth (height and diameter) were tracked for eleven years after release for four conifer species: noble fir (*Abies procera*), Douglas-fir (*Pseudotsuga menziesii*), Pacific silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*). Our overall objective was to examine how relative crown position, i.e., tree crown relative to *Ceanothus* crown, affected tree growth before and after removal of *Ceanothus*.

2. Materials and methods

2.1. Study site and measurements

The study area is on the southern slopes of Trout Creek Hill (elevation 790 m), a quaternary-aged shield volcano, within the Wind River Experimental Forest in the Gifford Pinchot National Forest, on the western side of the southern Washington Cascades. Conifers in the surrounding old-growth forest include Douglas-fir, western hemlock, western redcedar (*Thuja plicata*), Pacific yew (*Taxus brevifolia*), Pacific silver fir, grand fir (*Abies grandis*), and noble fir (Shaw et al., 2004).

This region has a wet climate with dry summers; over 90% of the 2820 mm annual precipitation falls during the 8-month period from October 1 to May 31 (climate data from the PRISM model developed by Daly et al., 1994 and available on-line at: http://www.ocs.orst.edu/prism/). Snow is common during the winter. The mean annual temperature is 8.7 °C, with a mean minimum January temperature of −2.8 °C and a mean maximum August temperature of 26.0 °C. Soils are uniformly deep loams derived from residual material weathered from andesites and basalts. Slopes range from 20 to 50%.

In 1978, the old-growth stand present on the unit was harvested and the area was broadcast burned in May 1979. A series of 0.4-ha plots was established and the area was planted in spring 1980 with conifer species in single and dual-species plots. Assignment of species, species-mixture type, and spacing to plots was random. Of the plots used in this study (see below), noble fir was planted in 13 plots (3 as dual-species plots), Pacific silver fir in 7 plots (4 as dual-species plots), Douglas-fir in 6 plots (4 as dual-species plots), and western hemlock in 3 plots (2 as dual-species plots). For dual- and single-species plots other than noble fir, spacing was at 3 m. Spacing for single-species plots of noble fir varied from 2 to 6 m. Survival of planted trees was high (>90%), however, some replanting was done from 1981 to 1984 to ensure the research plots were established at the targeted stand densities. Vegetation on the plots at the time of planting included California hazel, Pacific dogwood, vine maple, trailing blackberry, snowberry, salal, Oregon grape, huckleberry, beargrass, lupine, wood groundsel, vanilla leaf, and false Solomon's seal. Although *Ceanothus* is native to the region, it

Fig. 1. Aerial photo of the Trout Creek Hill research plantation in 1990, showing the extent and variation of *Ceanothus* encroachment on the 0.4-ha plots. *Ceanothus* appears as medium colored grey patches that generally are larger than individual conifer crowns shown in a darker grey.

was not evident in the old-growth stand prior to harvest, during planting, or the year after planting.

By 1985 *Ceanothus* was widely distributed on the lower (southern) portion of the plantation and by 1990 had overtopped many of the planted trees (Fig. 1). In May 1990, trees were released from potential competition with *Ceanothus* by manually clearing a 1-m radius area (3.14 m^2) around each tree. Note that all trees with *Ceanothus* in their neighborhoods were cleared of shrubs. Hence post-release comparisons are not made against "control" unreleased trees, as is common in many release experiments. Prior to release, individual trees, which differed markedly in their size and the type of interaction with *Ceanothus*, were assigned one of seven relative crown-positions (Fig. 2) based on visual assessment of contact between the tree and the neighboring *Ceanothus*. While these classes were assigned in 1990, we call these the 1989 relative crown positions to indicate status at the end of that growing season. Open-grown trees (relative crown position OG), may have had *Ceanothus* growing nearby, but not closely enough to result in aboveground contact or to provide mid-day shade. Thus the term 'open-grown' does not necessarily mean a tree was free from competition for water or nutrients. Occasionally other potentially competing species (e.g., vine maple) grew adjacent to planted conifers; trees having interactions with shrubs other than *Ceanothus* were not included in this analysis. Based on the tree heights within the relative crown positions before *Ceanothus* removal, we estimate that *Ceanothus* was at least 1.5 m tall by 1990. Thus, although *Ceanothus* was not noted the year after planting, it is likely that burning stimulated the seeds in the soil seed bank to germinate (Noste and Bushey, 1987) and the resulting plants grew rapidly.

Tree height was measured periodically over a 12-year period: at the end of the 1989, 1992, 1997, and 2001 growing seasons. Diameter at breast height (dbh) was measured at 1.3 m above groundline in 1992, 1997, and 2001 (many trees had not reached 1.3 m by 1989). In 1997, trees were again coded for type of interaction with *Ceanothus*, but not thereafter. At all measurement periods, damage was recorded and trees with top damage or those that died were excluded from analyses. Tree mortality was relatively low (6.8%) and proportional to the number of trees in each species-by-crown-position class; thus, eliminating dead trees did not bias our interpretation of the results. We used 2495 trees in the analysis: 1058 noble fir, 760 Douglas-fir, 403 Pacific silver fir, and 274 western hemlock (see Table 1).

2.2. Hypotheses and data analysis

We constructed a series of hypotheses to examine how growth might be affected by different *Ceanothus*–conifer interactions (Fig. 2). The first set of analyses used height at the time of release (May 1990, representing growth through the 1989 season) as the response variable. The relevant hypothesis and contrasts are:

H1: Growth will be greater for trees with 3 or more years of leader's growth above *Ceanothus* (L_A3) than for open-grown trees (OG). "*Some interaction is beneficial.*" If H1 is true (i.e., the null hypothesis is rejected), (L_A3 − OG) will be >0.

H2: Growth will be less for a tree completely overtopped by *Ceanothus* (L_BC) compared to open-grown trees (OG).

Table 1
Mean tree height (m) at the end of the 1989 growing season and sample size (in parenthesis) by relative crown position in 1989 averaged over all plots for the four conifer species at Trout Creek Hill, WA

Species	Relative crown position							
	OG	L_A3	L_A1	L_AS	L_BS	L_B	L_BC	All
Noble fir	1.7 (275)	2.3 (89)	2.0 (88)	2.0 (201)	1.5 (164)	1.4 (131)	1.2 (110)	1.7 (1058)
Douglas-fir	3.4 (251)	4.0 (153)	2.9 (44)	3.7 (248)	1.6 (28)	1.5 (17)	1.6 (19)	3.4 (760)
Pacific silver fir	1.2 (75)	2.0 (18)	1.6 (28)	1.6 (33)	1.2 (63)	1.0 (88)	0.9 (98)	1.2 (403)
Western hemlock	1.9 (62)	3.3 (23)	2.6 (9)	2.2 (43)	1.3 (45)	1.4 (39)	1.3 (53)	1.8 (274)

See Fig. 2 for an explanation of the codes for relative crown positions.

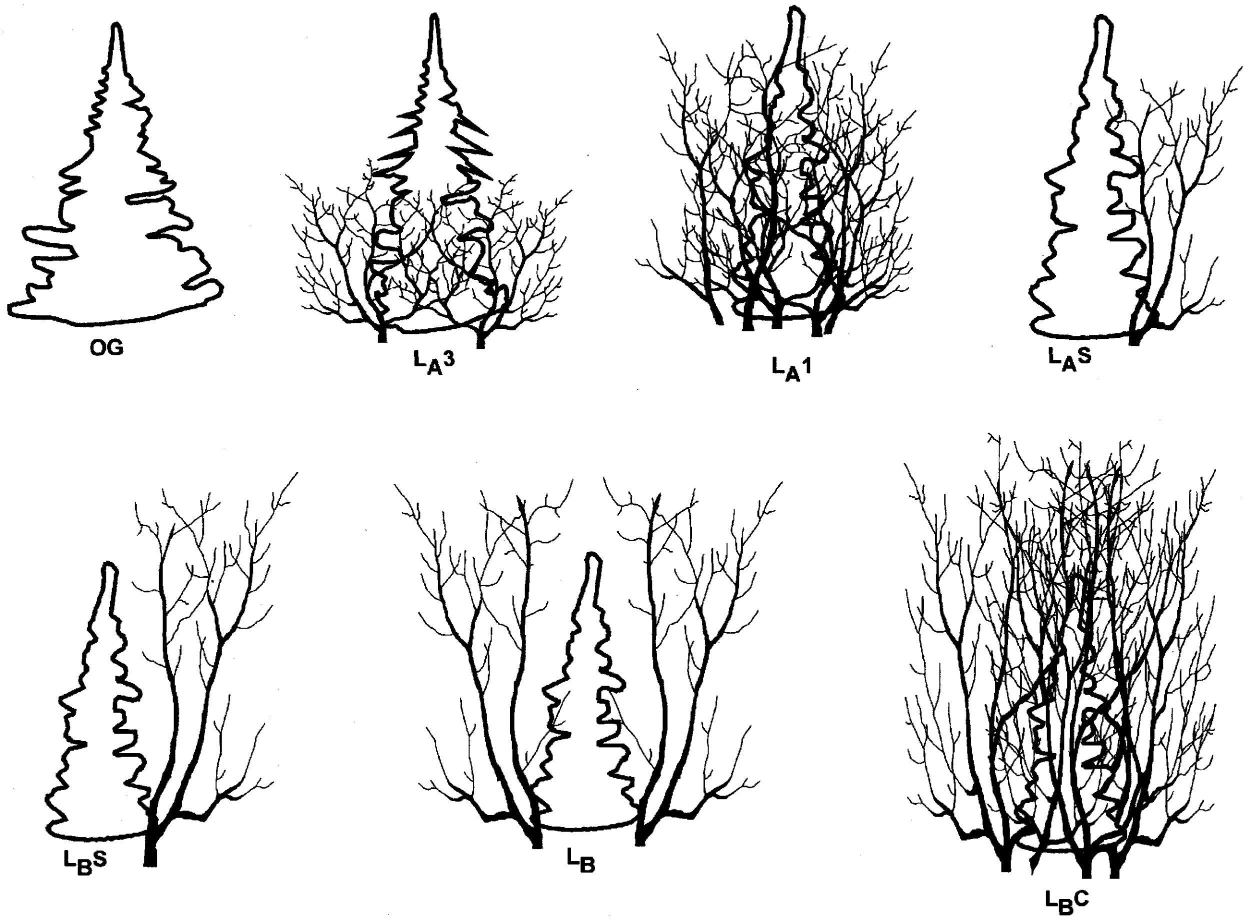

Fig. 2. Schematic showing relative crown positions and codes for the planted conifers and the naturally occurring *Ceanothus*. OG, open-grown; L_A3, leader 3 or more years above *Ceanothus*; L_A1, current leader above *Ceanothus*; L_AS, leader above *Ceanothus* canopy and *Ceanothus* only on one side; L_BS, leader below *Ceanothus* canopy and *Ceanothus* only on one side; L_B, leader below *Ceanothus* canopy and not directly covered, L_BC, leader below *Ceanothus* canopy and directly covered (note this figure is only intended to show crown interactions with the conifer and the shrub; crown depth or form are not implied).

"*Excessive interaction is detrimental.*" If H2 is true, (L_BC − OG) will be <0.

H3: Growth will be greater when leaders are 3 or more years in growth above *Ceanothus* (L_A3) versus only the current leader (L_A1). "*The amount of top exposed matters.*" If H3 is true, ($L_A3 - L_A1$) will be >0.

H4: For trees with *Ceanothus* growing on one side, growth will be lower when the leader is below (L_BS) versus when the leader is above *Ceanothus* (L_AS). "*With lateral interactions, the amount of top exposed matters.*" If H4 is true, ($L_BS - L_AS$) will be <0.

H5: Growth will be greater for a tree that is overtopped by *Ceanothus* and the leader is not directly covered (L_B) versus a tree that is overtopped and the leader is directly covered by *Ceanothus* (L_BC). "*When overtopped, exposure of the leader matters.*" If H5 is true, ($L_B - L_BC$) will be >0.

H6: Growth differences will be largest between trees where leaders have growth 3 or more years above *Ceanothus* (L_A3) and trees that are overtopped and directly covered by *Ceanothus* (L_BC). "*Ceanothus enhances and suppresses growth depending on its crown position relative to the trees.*" If H6 is true, the value of ($L_A3 - L_BC$) will be larger than the values in the other comparisons.

H7: For trees with the leader above *Ceanothus*, growth will be greater when *Ceanothus* grows on one side (L_AS) than when *Ceanothus* surrounds the tree (L_A1). "*Lateral exposure matters.*" If H7 is true, ($L_A1 - L_AS$) will be <0.

For the period in the study (through 2001) tree-to-tree interactions were considered minimal on all plots, i.e., planted tree spacing did not have a significant effect on tree growth (data on file, Pacific Northwest Research Station, Olympia, WA). Nonetheless, due to the original experimental design (which determined the location of tree species across the unit and variation in tree spacing among plots), the variation in *Ceanothus* cover among plots, the unequal distribution of crown position classes among plots, and the different sample sizes within the crown position classes among plots, we summarized the data separately by species and plot. For these analyses, individual trees are experimental units and the treatments are the crown position classes that developed as a

Table 2
Mean effect sizes for the seven hypotheses on 1989 tree heights (+half-width 95% confidence intervals) for the four conifer species

Species	Hypothesis code						
	H1 (L_A3-OG)	H2 (L_BC-OG)	H3 (L_A3-L_A1)	H4 (L_BS-L_AS)	H5 (L_B–L_BC)	H6 (L_A3-L_BC)	H7 (L_A1-L_AS)
Noble fir	***0.77 (0.25)***	***−0.87 (0.25)***	***0.62 (0.33)***	***−1.03 (0.23)***	***0.49 (0.28)***	***1.79 (0.36)***	−0.01 (0.27)
Douglas-fir	***0.27 (0.24)***	***−1.44 (0.68)***	***0.91 (0.39)***	***−1.33 (0.57)***	0.37 (0.99)	***2.45 (0.65)***	***−0.64 (0.36)***
Pacific silver fir	***1.27 (0.58)***	***−0.52 (0.37)***	0.53 (0.65)	***−0.95 (0.48)***	0.03 (0.31)	***1.83 (0.65)***	0.17 (0.54)
Western hemlock	***1.58 (0.60)***	***−1.00 (0.44)***	***1.05 (1.0)***	***−1.21 (0.46)***	0.37 (0.44)	***3.91 (0.84)***	0.13 (0.90)

Effects in bolded italics are significantly different from 0. See text for explanation of hypotheses and associated contrasts.

result of natural processes. We then used meta-analysis (Cooper and Hedges, 1994) to get composite (across plot) estimates of relative crown position effects and associated measurement error. The seven hypotheses were tested for each species by applying the contrast statements (difference between the specified pair of crown positions) to the plots where each species was planted. A standardized effect size (g) for each contrast and species was then calculated as the difference divided by a pooled estimate of the variance from the plot (Wang and Bushman, 1999). The standardized effect size and the 95% confidence interval were graphed for each contrast and species (we present these graphs for H1 and H2) and then examined visually.

In addition to the seven hypotheses tested for each species, we also hypothesized that responses might vary among species due to differences in their shade tolerance. For instance, we hypothesized that excessive interaction (H2) would be less detrimental to growth for the shade-tolerant western hemlock or Pacific silver fir compared with the shade-intolerant Douglas-fir; since noble fir is intermediate in shade tolerance, we hypothesized it would be intermediate in its tolerance of excessive interaction. To facilitate comparisons among species, we calculated an overall mean effect by species for each contrast; as before, the species means were weighted based on within-plot variance.

We also assessed how height in 2001 and diameters in 1992, 1997, and 2001 changed based on 1989 crown position for each species. To avoid biases associated with changes in sample sizes from not measuring diameter on trees less than 1.3 m tall in 1992, we only used trees that had a dbh recorded in 1992 in the 1997 and 2001 analyses of dbh. For the 2001 height data, while we applied the same contrasts as for the 1989 data, our main goal was to assess whether the general patterns of *Ceanothus*–tree interactions remain after release.

3. Results

3.1. Pre-release (1989)

Ten years after planting, mean tree heights differed among the species, ranging from 0.9 to 4.0 m, and depended on relative crown position (Table 1). Considering all crown positions, mean tree heights ranked: Douglas-fir (individual tree heights ranging from 0.35 to 7.70 m) > western hemlock (range: 0.25–4.90 m) > noble fir (range: 0.25–4.20 m) > Pacific silver fir (range: 0.15–3.55 m) (Table 1). For the four species, tree heights were greatest for trees with 3 or more years of leader growth above *Ceanothus* (L_A3) and lowest for trees that were overtopped by *Ceanothus* (L_B and L_BC). The second greatest tree heights were found for trees with leaders either above a side-growing *Ceanothus* (Douglas-fir, L_AS) or above *Ceanothus* surrounding the tree (western hemlock, L_A1), or with either of these conditions (the true firs, L_AS and L_A1).

Prior to release, four of the hypotheses (H1, H2, H4, and H6) were true (the null hypotheses were rejected) for all four species (Fig. 3 for H1 and H2 by plot and species, Table 2), and indicate that not only does the type of crown interaction with *Ceanothus* influence tree growth, but that positive and negative growth effects occurred depending on the interaction. For example, H1 "*Some interaction is beneficial*", which predicts that heights of trees with growth 3 or more years above *Ceanothus* will be greater than those of open-grown trees, and H2 "*Excessive interaction is detrimental*", which predicts that heights of trees overtopped by *Ceanothus* will be less than those of open-grown trees, were supported for all four species (Fig. 3, Table 2). Shade-intolerant Douglas-fir exhibited the smallest benefit from interacting with *Ceanothus* (H1), roughly an 18% growth enhancement[1] over open-grown trees, and exhibited the largest growth reduction, about 53%, from being overtopped by *Ceanothus* (H2). In contrast, shade-tolerant western hemlock exhibited at least a 70% growth increase for trees with growth 3 or more years above *Ceanothus* (H1) and only a 30% reduction in growth when overtopped by *Ceanothus* (H2), compared to open-grown trees. Similarly, shade-tolerant Pacific silver fir showed a relatively large (67%) increase in height from interacting with *Ceanothus* (H1) and only a 22% reduction in height when overtopped by *Ceanothus* (H2). Height growth of noble fir, moderately shade tolerant, increased by about 35% when associated with *Ceanothus* (H1), and was reduced by about 30% when overtopped by *Ceanothus* (H2). Apparently, even if *Ceanothus* only grows to the side of a tree, heights were reduced for all species when *Ceanothus* covers the

[1] Calculated from data in Table 1 as $((L_A3 - OG)/OG) \times 100$. Subsequent calculations of percent change in growth as enhancement or reduction follow the same format.

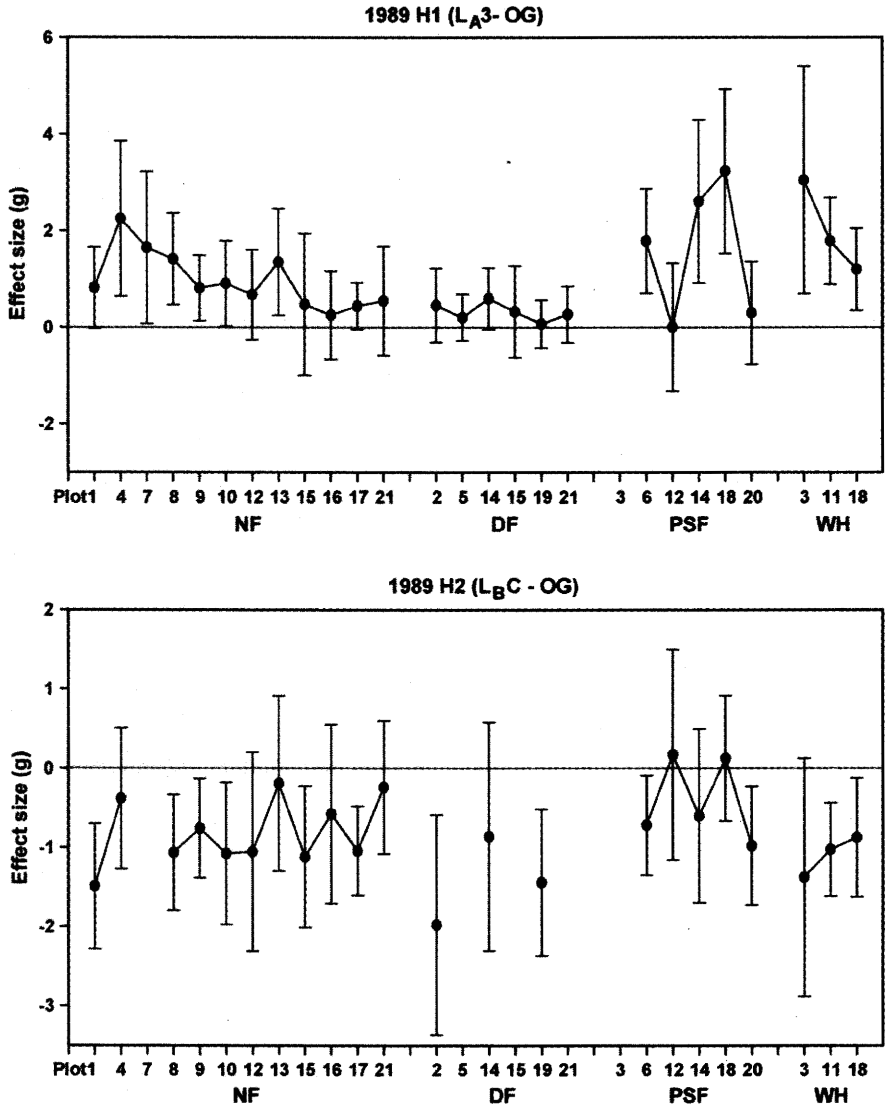

Fig. 3. Plot-level results by conifer species for H1 and H2 (based on height at time of release). NF, noble fir; DF, Douglas-fir; PSF, Pacific silver fir, and WH, western hemlock. Bars show the 95% confidence interval of the effect size. Plots without points on the graph represent crown position classes with insufficient sample sizes for analysis. See text for a description of H1 and H2.

leader (H4), suggesting again that negative interactions are largely driven by whether the leader is exposed or not. H6, which predicts that the largest differences in growth will be found between expected detrimental and beneficial *Ceanothus* interactions, was supported across all four species, as indicated by the largest mean effect (Table 2).

For all conifers, growth was greater for trees with 3 or more years of leader growth above *Ceanothus* versus those trees with only the current leader above *Ceanothus* (H3), although the effect was not significant for Pacific silver fir (Table 2). A minimal amount of solar exposure to overtopped trees yielded a significantly positive growth response (H5) only for noble fir, and the response was relatively small (Table 2). Finally, for trees with leaders just above *Ceanothus,* lateral exposure to the sun increased growth (H7) only for Douglas-fir (Table 2).

3.2. Post-release (through 2001)

In 2001, mean tree heights of the species ranged from 6.2 to 12.5 m (Table 3). As in 1989, 2001 mean tree heights ranked: Douglas-fir (individual heights ranging from 1.3 to 19.8 m) > western hemlock (range: 3.0–13.2 m) > noble fir (range: 0.9–14.5 m) > Pacific silver fir (range: 0.8–11.9 m) (Table 3). For all species, tree heights in 2001 were greatest for trees with 3 or more years of leader growth above *Ceanothus* by the end of 1989 (L_A3) (note for Pacific silver fir the trees with leaders above a side-growing *Ceanothus* (L_AS) were equal in height to those coded L_A3) and lowest for trees that were overtopped by *Ceanothus* by the end of 1989 (L_B, L_BC). These were the same classes that were ranked lowest and highest based on the pre-release height data.

Table 3
Mean tree height (m) at the end of the 2001 growing season and sample size (in parenthesis) by 1989 relative crown position averaged over all plots for the four conifer species

Species	Relative crown position							
	OG	L_A3	L_A1	L_AS	L_BS	L_B	L_BC	All
Noble fir	8.1 (264)	9.5 (87)	8.2 (84)	8.8 (188)	7.0 (157)	6.5 (124)	4.7 (103)	7.7 (1007)
Douglas-fir	12.5 (131)	13.5 (68)	11.2 (18)	13.3 (132)	9.1 (17)	8.4 (12)	8.6 (9)	12.5 (387)
Pacific silver fir	6.6 (54)	8.4 (13)	7.6 (20)	8.5 (19)	6.5 (44)	5.3 (52)	4.7 (54)	6.2 (256)
Western hemlock	8.9 (27)	10.9 (13)	8.5 (4)	9.2 (17)	7.3 (15)	7.2 (8)	7.2 (13)	8.6 (97)

See text and Fig. 2 for an explanation of the codes for relative crown positions.

Table 4
Mean effect sizes for the seven hypotheses on 2001 tree heights (+half-width 95% confidence intervals) for the four conifer species

Species	Hypothesis code						
	H1 (L_A3 – OG)	H2 (L_BC – OG)	H3 (L_A3 – L_A1)	H4 (L_BS – L_AS)	H5 (L_B – L_BC)	H6 (L_A3 – L_BC)	H7 (L_A1 – L_AS)
Noble fir	***0.52 (0.25)***	***−1.30 (0.26)***	***0.80 (0.34)***	***−1.01 (0.23)***	***0.76 (0.30)***	***2.01 (0.38)***	***−0.36 (0.28)***
Douglas-fir	−0.09 (0.36)	***−1.64 (1.33)***	0.17 (0.68)	***−2.50 (1.09)***	ins[a]	***3.00 (1.19)***	−0.40 (0.65)
Pacific silver fir	***0.73 (0.64)***	***−0.66 (0.50)***	0.47 (0.88)	***−1.39 (0.69)***	0.27 (0.41)	***1.38 (0.79)***	−0.49 (0.76)
Western hemlock	***0.87 (0.77)***	−0.70 (0.88)	***2.79 (2.25)***	***−1.13 (0.79)***	0.85 (1.22)	***1.02 (0.91)***	−0.65 (1.53)

Effects in bolded italics are significantly different from 0. See text for explanation of hypotheses and associated contrasts.
[a] ins, insufficient data for meta-analysis.

In 2001, similar to the pre-release pattern, H4 and H6 were true for all species and indicate that positive and negative growth effects were still noted up to twelve years after release and depended somewhat on relative crown position in 1989 (Table 4). H1, the "*Some interaction is beneficial*" hypothesis, which was true for all species in 1989 (though the effect was small for shade-intolerant Douglas-fir), after release, was true for all species in 2001 except for Douglas-fir. H2, "*Excessive interaction is detrimental*", which was true for all species in 1989, was no longer statistically significant in 2001 for western hemlock.

Increase in height over the 12 years (1989–2001) after release was influenced by relative crown position in 1989 and by differences in shade tolerance and inherent growth rates for the species (Fig. 4). For all four conifer species, heights were greater for trees with leaders exposed (relative crown positions OG, L_A3, L_A1, L_AS) prior to release, than for those with leaders covered (relative crown positions L_BS, L_B, L_BC) prior to release. Previously overtopped trees did not catch up in size with non-overtopped trees; however, the responses seemed to fall into two categories. For the two fastest growing species, Douglas-fir and western hemlock, the differences in heights among the relative crown positions remained fairly consistent from 1992 to 2001 (Fig. 4); thus, the growth rates were similar across the classes. For the true firs, however, the range in heights among the relative crown positions diverged between 1992 and 2001, with the greatest change in height occurring for the trees with leaders exposed at the time of release. Changes in dbh after release (Fig. 5), revealed a pattern similar to that for changes in height in that trees with leaders exposed prior to release attained the largest diameters in 1992, 1997, and 2001 and there was little relative shift in diameter among the 1989 crown position classes throughout the post-release period. The range in diameters among the crown position classes was greater in 2001 than in 1992, indicating that the trees with exposed leaders prior to release grew more in diameter than trees without exposed leaders (Fig. 5). This effect was smallest for Pacific silver fir, the slowest growing and most shade tolerant of the four conifers.

By 1997 (the last year crown positions were recorded), *Ceanothus* and other shrubs had returned into many of the 3.14 m^2 clearings either by growth of adjacent plants or coppice growth from cut stumps; thus, seven years after clearing about 50% of the original trees covered by *Ceanothus* were again covered by competing vegetation (Table 5). This effect was most common for the slow growing Pacific silver fir, where 32% of the trees were below *Ceanothus* in 1997, versus only 3.5% for Douglas-fir.

Table 5
Number of trees by species in the relative crown positions in 1997, the last year crown position data was collected

Species	Relative crown position							
	OG	L_A3	L_A1	L_AS	L_BS	L_B	L_BC	All
Noble fir	41	519	139	153	52	74	54	1032
Douglas-fir	66	424	28	190	14	5	7	734
Pacific silver fir	17	112	91	44	22	47	55	388
Western hemlock	11	130	36	35	29	11	27	279

These data are based on canopy interactions with *Ceanothus* as well as other woody shrubs and are shown to indicate growth into the area originally cleared of *Ceanothus*. See Fig. 2 for an explanation of the codes for relative crown positions.

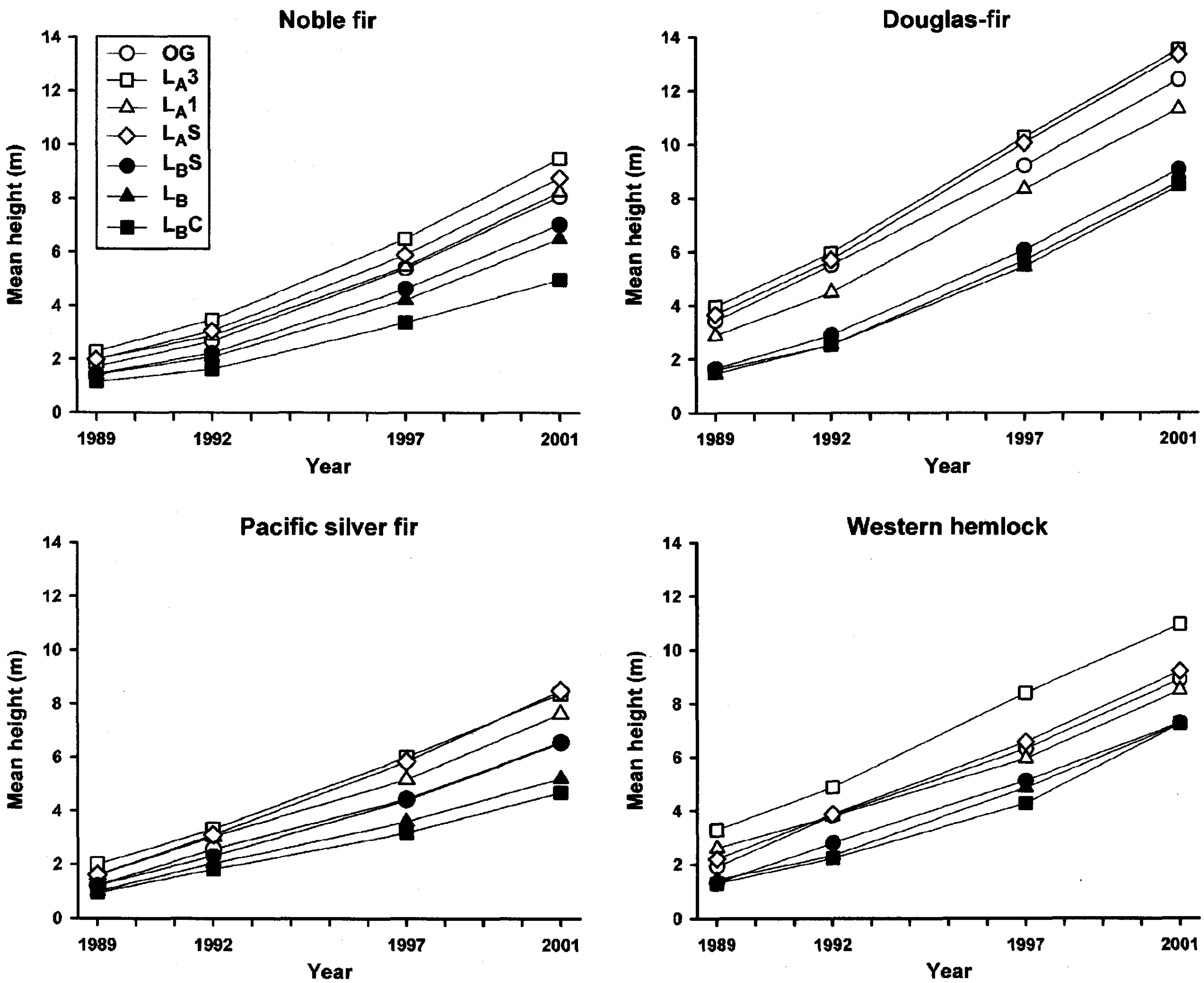

Fig. 4. Height from 1989 to 2001 by tree species and relative crown position in 1989. Crown positions where the leader was exposed (OG, L_A3, L_A1, L_AS) are shown with open symbols and those where the leader was covered (L_BS, L_B and L_BC) are shown with filled symbols.

4. Discussion

4.1. Positive and negative effects of Ceanothus on conifer growth prior to release

Height growth of four conifer tree species ten years after planting was both positively and negatively affected by *Ceanothus*, with the direction and magnitude of response depending on the type of canopy interaction between an individual tree and *Ceanothus*. For all species, when the leader remained above a *Ceanothus* crown, tree growth was generally enhanced relative to open-grown trees and to trees with leaders below a *Ceanothus* canopy. Similarly, for all species, when the leader remained below a *Ceanothus* crown, height growth was less than for open-grown trees. Thus we show that tree–*Ceanothus* interactions at the individual tree scale are important for determining positive or negative effects on growth. This is consistent with others who have used neighborhood approaches to examine competitive interactions. For example, Wagner and Radosevich (1998) found that including heights of neighboring shrubs (primarily *Rubus spectabilis*) significantly improved the performance of height growth models for Douglas-fir in the Oregon Coast Range. They found that height growth of Douglas-fir seedlings was reduced when woody neighbors overtopped the seedlings and that non-intermingling crowns had little effect on growth. While mean foliar cover across a stand may be a practical measure of competition (cf. McDonald and Fiddler, 1989), it will likely not reveal the underlying heterogeneity of tree–shrub interactions and the consequences this has for competitive outcomes.

Many studies have documented negative effects of *Ceanothus* on conifer growth (e.g., Zavitkovski et al., 1969; Monleon et al., 1999), attributable to competition for light (Conard, 1985), soil moisture (Petersen, 1980; Conard and Radosevich, 1982; Petersen et al., 1988), and nutrients (Powers and Reynolds, 1999). Yet few studies have shown positive effects of growing with *Ceanothus*. Youngberg (1966) describes the "thrifty" growing conditions of ponderosa pine seedlings growing in snowbrush clumps, but provides no growth data. Scott (1970) and Horowitz (1982), show conifers growing on the edges of *Ceanothus* patches in the central OR Cascade Mountains benefit from the interaction. Scott (1970)

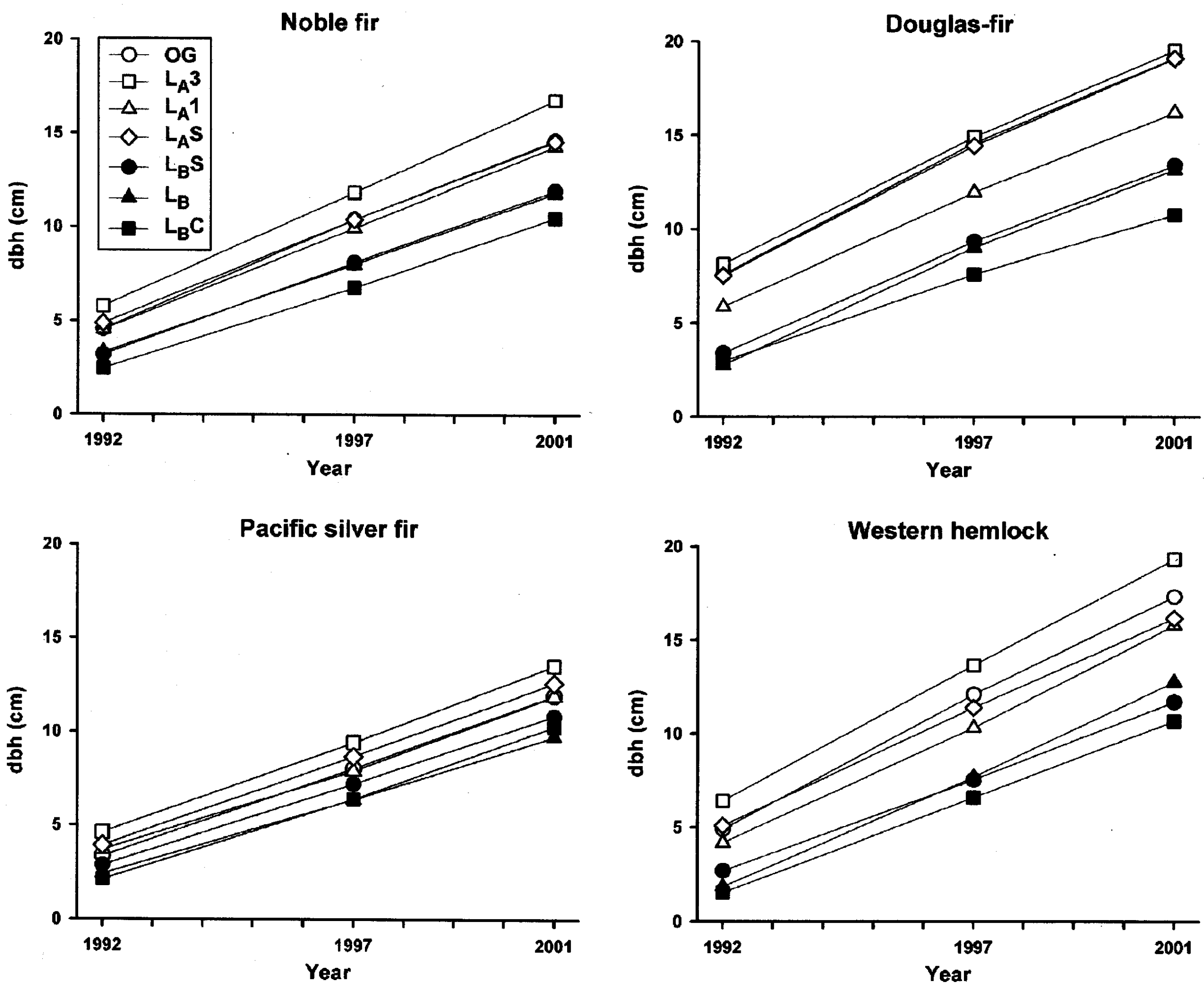

Fig. 5. Tree diameter at breast height from 1992 to 2001 by tree species and relative crown position in 1989. Crown positions where the leader was exposed (OG, L_A3, L_A1, L_AS) are shown with open symbols and those where the leader was covered (L_BS, L_B and L_BC) are shown with filled symbols.

found that open-grown seedlings were prone to browse damage which likely explained their low heights relative to seedlings growing near the edges of or directly under *Ceanothus* patches. We did not find significant browse damage at Trout Creek Hill. Scott (1970) suggests that seedlings growing directly under *Ceanothus*, which were also shorter than seedlings near the edges, may have suffered from light and moisture competition. Both of these studies took neighborhood approaches, suggesting again that a reliance on stand level averages may mask cases where growth enhancement occurs. In other cases, trees were not selected if they were taller than *Ceanothus* (e.g., Petersen et al., 1988) or stands were more extensively and consistently encroached by *Ceanothus* (e.g., Gratkowski and Lauterbach, 1974) than we found at Trout Creek Hill, perhaps explaining why these particular studies failed to show positive effects of growing with *Ceanothus*.

Ceanothus can facilitate growth of young conifers via several mechanisms. Conifer seedlings growing under *Ceanothus* benefit from cooler air and soil temperatures (Youngberg, 1966; Scott, 1970; Jones, 1995), increased surface soil moisture (Scott, 1970), and shading, the latter protecting against winter desiccation and excessive radiation loading (Conard and Radosevich, 1982). All of these factors were probably advantageous during the juvenile stages of growth on the south-facing slopes of Trout Creek Hill. However, these benefits may not be specific to *Ceanothus* and could have been provided by other shrub species (Youngberg, 1966; Busse et al., 1996). For example, soil N was greater under N fixing and non-N fixing shrubs compared to open areas (Busse et al., 1996) and lower surface soil temperatures were found under any structure providing shade (Conard and Radosevich, 1982). Nonetheless, because many studies have documented atmospheric N_2 fixation for *Ceanothus* (e.g., Binkley et al., 1982; McNabb and Cromack, 1983; Busse, 2000), we should not discount the role that *Ceanothus* may play leading to greater local soil N availability. Several trials in the Wind River area have demonstrated positive conifer growth responses to N additions (e.g., Miller and Tarrant, 1983; DeBell et al., 2002) and enhanced Douglas-fir growth in association with red alder (Miller and Murray, 1978; Binkley, 2003), another species that symbiotically fixes N. While we did not measure soil N availability at Trout Creek Hill, collectively these studies indicate the potential for conifers to benefit from fixation-related increases in soil N availability from *Ceanothus*.

Differences in shade tolerance and growth rates among the conifer species may have influenced species-specific interactions with *Ceanothus*. Douglas-fir, the least shade-tolerant of the four species, had the smallest growth benefit from interacting with *Ceanothus*, the largest growth suppression (53%) from being overtopped by *Ceanothus*, and was the only species to show a positive growth response to lateral solar exposure. A larger proportion of Douglas-fir seedlings (nearly 60%, Table 1) was already taller than *Ceanothus* by 1989 compared with the other species (<40%). This suggests that on this site, the rapidly growing Douglas-firs were able to outgrow *Ceanothus* in height, in most cases remaining above its canopy. When Douglas-fir was overtopped by *Ceanothus*, because of its intolerance to shade, height growth was significantly reduced, albeit happening infrequently (percentage of seedlings below *Ceanothus* before cutting was 8% for Douglas-fir versus 38, 62, and 50% for noble fir, silver fir and western hemlock, respectively). Noble fir, classified as moderately shade-tolerant, had the next smallest growth benefit from interacting with *Ceanothus*, ranked second in the proportion of its trees above *Ceanothus*, and its growth was reduced by about 30% under *Ceanothus*. We found that shade-tolerant Pacific silver fir and western hemlock showed the greatest growth benefit from interacting with *Ceanothus*, although for these species, less than 30% of their seedlings were above *Ceanothus* at the time of release. The most shade-tolerant species, Pacific silver fir, had the least reduction in height under *Ceanothus*, yet because of its slow growth, most of its seedlings were found growing under *Ceanothus*.

Height is often considered somewhat insensitive to competition relative to radial growth (McDonald and Fiddler, 1989; Wagner and Radosevich, 1998; Richardson et al., 1999). Ideally we would have compared the patterns of diameter and height growth for the various relative crown positions before *Ceanothus* was removed. However, in 1990, when the first assessment of crown interaction was made (and just prior to *Ceanothus* removal), most of the trees were below the height (1.3 m) where diameter was measured so we did not have enough data to analyze. Nonetheless, we found significant height sensitivity to competition, as has been found elsewhere when tree leaders are overtopped by woody neighbors (cf. Wagner and Radosevich, 1998).

4.2. Patterns of growth after Ceanothus removal

Similar patterns in diameter and height growth among the crown positions twelve years after release from *Ceanothus* indicate that the manual clearing did little to change the relative rankings of the original crown positions, i.e., trees with exposed leaders before release were always taller and had greater diameters than trees without exposed leaders. In general, the differences in height among the crown positions after release (1992, 1997, and 2001) were relatively constant over time for Douglas-fir and western hemlock but increased over time for the true firs (Fig. 4). This suggests that the effects of the previous interactions with *Ceanothus* were longer lasting for the true firs than for the other two species.

There are several reasons that might explain the continued differences in growth after release among the relative crown position classes for the true firs. Height growth rates for true firs are relatively low below heights of 1.3–1.5 m (Harrington and Murray, 1982), suggesting that even after release, growth rates remain low for individuals <1.5 m. A sudden exposure to sun after release also can cause additional growth suppression (Petersen, 1980); this effect could be exacerbated in true firs because their longer retention of foliage compared to Douglas-fir and western hemlock (Minore, 1979) might delay adaptation to a new microenvironment. Conard and Radosevich (1982) show that providing artificial shade in conjunction with removing shrubs tended to alleviate the short-term diminishment of growth of white fir. Although the trees at Trout Creek Hill grew on a southerly aspect, and release generally would increase solar exposure, the relatively small (1 m radius) area cleared around the trees maintained some shading; a much less extreme change compared with removing shrubs from a larger area. Another possible cause for the increased growth suppression of the true firs was the return of *Ceanothus* and other woody shrubs into about half of areas cleared of *Ceanothus* in 1990. The sizes of clearings to remove potentially competing vegetation vary across and within studies. Jaramillo (1988) found that the response of Douglas-fir to clearing was proportional to the size of the clearing (ranging from 1.2 to 3.7 m in radius). Collectively, these findings suggest that some of the shorter slow growing true firs were unable to increase in height growth quickly enough to profit from the short-term opening made available with the hand-release operation. It is not known, however, what the longevity or magnitude of long-term responses will be. Several studies found a diminishing effect of shrub competition on tree growth with stand age (Busse et al., 1996) or stand development (Oren et al., 1987).

Analyzing tree growth data by height class at the time of release, rather than by crown position, is potentially another way to examine the effect of clearing on growth. Height and diameter in 2001 were strongly related to height in 1989 across species (data not shown, Pearson correlation coefficients, $r > 0.81$ for both variables and all species) and across crown position classes, suggesting that the responses after clearing were primarily a function of height in 1989. Thus, relative crown position had a direct effect on height in 1989 and an indirect effect on height and diameter growth after release for the reasons previously discussed.

4.3. Conclusion and management implications

Both positive and negative effects of growing in association with *Ceanothus* were found for diameter and height growth of the four conifer species, with the nature and extent of the response depending on the type of interaction between the conifer and *Ceanothus* and the inherent growth rates and shade tolerances of the tree species. For all conifer species, if the leader was above the *Ceanothus* canopy, growth of the associated tree was greater than growth of open-grown trees, and if the leader was below the *Ceanothus* canopy, respective growth was less than for open-grown trees. Cutting *Ceanothus* appears to benefit height growth of overtopped Douglas-fir and western hemlock more so than for overtopped true firs.

Our findings from the plantation in western Washington suggest that forest managers interested in maximizing tree growth could permit and even encourage *Ceanothus* coexistence as long as the conifer leaders remained above the shrubs; but they might consider removing *Ceanothus* if it appeared that the tree leaders would be overtopped. Also, if *Ceanothus* were to be removed by manual cutting, the size of the opening should be larger for species with slow juvenile growth than for more rapidly growing species to avoid any *Ceanothus* re-growth from overtopping these trees. Managers considering releasing conifers from *Ceanothus* encroachment need to consider tree species, the proportion of trees that are currently or will be overtopped by *Ceanothus*, and longer-term growth responses.

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