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# Hydraulic architecture and photosynthetic capacity as constraints on release from suppression in Douglas-fir and western hemlock

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**Summary** We compared hydraulic architecture, photosynthesis and growth in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a shade-intolerant species, and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), a shade-tolerant species, to study the temporal pattern of release from suppressive shade. In particular, we sought to determine whether hydraulic architecture or photosynthetic capacity is most important in constraining release. The study was conducted at two sites with mixed stands of 10- to 20-year-old Douglas-fir and western hemlock. At one site, the stand had been thinned allowing release of the understory trees, whereas at the other site, the stand remained unthinned. Douglas-fir had lower height growth (from 1998–2003) and lower relative height growth (height growth from 1998 to 2003/height in 1998) than western hemlock. However, relative height growth of released versus suppressed trees was higher in Douglas-fir (130%) than in western hemlock (65%), indicating that, although absolute height growth was less, Douglas-fir did release from suppression. Release seemed to be constrained initially by a limited photosynthetic capacity in both species. Five years after release, Douglas-fir trees had 14 times the leaf area and 1.5 times the leaf nitrogen concentration ($N_{area}$) of suppressed trees. Needles of released western hemlock trees had about twice the maximum assimilation rate ($A_{max}$) at ambient [$CO_2$] as needles of suppressed trees and exhibited no photoinhibition at the highest irradiances. After release, trees increased in leaf area, leaf N concentration and overall photosynthetic capacity. Subsequently, hydraulic architecture appeared to constrain release in Douglas-fir and, to a lesser extent, in western hemlock. Released trees had significantly less negative foliar $\delta^{13}C$ values than suppressed trees and showed a positive relationship between leaf area:sapwood area ratio ($A_L/A_S$) and $\delta^{13}C$, suggesting that trees with more leaf area for a given sapwood area experienced a stomatal limitation on carbon gain. Nonetheless, these changes had no significant effects on leaf specific conductivities of suppressed versus released trees of either species, but leaf specific root conductance was significantly lower in released Douglas-fir.

*Keywords: $A/C_i$ curves, advance regeneration, $\delta^{13}C$, leaf-specific conductivity, light-response curves, nitrogen content, root conductance.*

## Introduction

Understanding the mechanisms that allow understory saplings to release from suppression is important ecologically and silviculturally because suppressed saplings contribute substantially to the gap regeneration potential of natural forests. However, new gaps are rare in most natural forests (Canham 1989). For example, new gaps in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest make up about 0.7% of mature forests and 0.2% of old-growth forests (Spies et al. 1990). Nevertheless, understanding the mechanisms by which trees release from suppression is of increasing interest in the U.S. Pacific Northwest, where forestry practices are shifting from even-aged to uneven-aged stand management. Uneven-aged stand management systems favor partial cutting over clearcutting of stands. Therefore, regeneration is more likely to develop under an overstory. Species that quickly take advantage of gaps formed by thinning will outcompete slower responding neighbors.

There is uncertainty about how Douglas-fir, a moderately shade-intolerant, but commercially important, species will be affected by a shift in forestry practices from even- to uneven-aged systems. Douglas-fir has intermediate shade tolerance (Minore 1979) and normally regenerates in large gaps such as those created by a fire or by clearcutting (Franklin et al. 2002). Shade-tolerant species like western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Minore 1979) frequently regenerate under a canopy of mature trees, making suppression and release more common in this species (Munger 1940, Gray and Spies 1997, Franklin et al. 2002). There is some concern that uneven-aged stand management could shift species composition from less shade-tolerant, but high-value, species like Douglas-fir toward more shade-tolerant, lower-value tree species like western hemlock (Tesch and Korpela 1993). There-

fore, comparison of Douglas-fir and western hemlock both when suppressed and when released will help evaluate how readily Douglas-fir is released from suppression and whether concern about shifts in species composition is warranted.

In addition to determining how readily Douglas-fir and western hemlock are released from suppression, another objective of this study was to identify structural and physiological constraints on release. Douglas-fir exhibits a delay before showing evidence of release after thinning, indicating that there are structural or physiological changes that must occur before shoot growth rate increases (Staebler 1956, Van Pelt and Franklin 1999, Kneeshaw et al. 2002).

We examined two competing hypotheses about the relative importance of hydraulic architecture and photosynthetic capacity in constraining release from suppression. According to the first hypothesis, release from suppression following overstory thinning is initially constrained by the inability of the vascular system to compensate for increased water demand by the leaves. As a result, trees show no signs of release until a change in their hydraulic architecture has taken place. Hydraulic architecture determines the path of water movement from the roots to the leaves and the relationship between the cross-sectional area of water-conducting conduits (below- and aboveground) and the area of foliage they supply with water (Tyree and Ewers 1991, Cruiziat et al. 2002). Therefore, release from suppression, may depend on an increase in sapwood area or specific conductivity ($K_s$), or both, relative to leaf area. We have already shown that released Douglas-fir and western hemlock trees have significantly higher $K_s$ than suppressed trees (Renninger 2005, Table 1). Several studies have found that faster-growing trees have more leaf area for a given unit of sapwood area than slower-growing trees (Espinosa Bancalari et al. 1987, Thompson 1989, Mencuccini and Grace 1994). In addition to having a greater leaf area for a given amount of sapwood area, leaves of released trees may also have a greater demand for water than leaves of suppressed trees. Whitehead et al. (1996) found that sun needles of *Pinus radiata* D. Don had a higher stomatal conductance, and therefore a higher rate of transpiration, than shade needles. If this is true also for Douglas-fir and western hemlock, then water must be transported more efficiently to sun needles than to shade needles to maintain the same leaf water potentials ($\Psi$). Finally, Kneeshaw et al. (2002) found that lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir saplings showed water stress after overstory removal and they predicted that reduced height growth was not limited by carbon availability, but by limited water transport capacity.

A tree is constrained by hydraulic architecture if its root area and the conductivity of its root system are insufficient to supply water lost in transpiration while maintaining normal leaf water potentials. Newton and Cole (1991) compared shoot to root ratios in different size classes of Douglas-fir and found that the mean was around four, but only about one in severely suppressed trees. However, Eis (1974) observed that dominant trees had more symmetrical and well-developed root systems than either intermediate or suppressed individuals. Therefore, suppressed trees could be severely lacking in root area needed to acquire and transport water to their leaves after release.

The second hypothesis is that photosynthetic capacity constrains release. This hypothesis states that delays in release in Douglas-fir result from the time required for the tree to replace shade needles with sun needles having a higher photosynthetic capacity. In the context of this hypothesis, a comparison of Douglas-fir and western hemlock is of interest because these species exhibit different photosynthetic efficiencies depending on irradiance. For example, western hemlock has a lower mean light-saturated photosynthetic rate, light compensation point and dark respiration rate than Douglas-fir (Bond et al. 1999, Lewis et al. 2000). Lewis et al. (2000) found that western hemlock had higher net photosynthetic rates at lower irradiances, whereas Douglas-fir had higher net photosynthetic rates at higher irradiances. Douglas-fir and western hemlock also differ in patterns of carbon allocation. Douglas-fir allocates more carbon to stem biomass and less to foliage biomass than western hemlock (Mailly and Kimmins 1997). This means that, at the time of release, western hemlock may be better adapted than Douglas-fir to the post-release light conditions. Douglas-fir would then respond more slowly to release than western hemlock. Such a delay in response to release was reported in sapwood growth of white spruce (*Picea glauca* (Moench) Voss), which was attributed to the need for the reallocation of carbon to new foliage and roots before increased shoot growth was possible (Lieffers et al. 1993).

## Materials and methods

### *Site description*

The study was conducted at an approximately 30 ha site located in the Coast Range near Falls City, Oregon (44.82° N, 123.62° W, elevation 350 m), with a site index ($SI_{50}$) of 128. The site was thinned from 415 trees $ha^{-1}$ to 289 trees $ha^{-1}$ in 1978 to allow self-seeding of Douglas-fir and western hemlock. In 1998, a portion of the site (about 20 ha) was thinned again to a density of 99–148 trees $ha^{-1}$ releasing the Douglas-fir and western hemlock advance regeneration, whereas the adjacent portion of the site (about 10 ha) was left unthinned. Herbaceous vegetation in the understory consisted of bracken fern (*Pteridium aquilinum* (L.) Kuhn), sword fern (*Polystichum munitum* (Kaulf.) Presl.), Oregon grape (*Berberis nervosa* Pursh), salal (*Gaultheria shallon* Pursh), trailing blackberry (*Rubus hispidus* L.) and foxglove (*Digitalis purpurea* L.).

### *Tree selection and measurement*

In June and July 2004, we selected 10 trees of each species (Douglas-fir and western hemlock) from throughout each site (suppressed and released). We chose trees that we estimated to have been 1–2 m tall in 1998, were without visible damage to the bark, had no branches competing strongly for dominance with the terminal shoot. For each of the 40 trees, we measured current height and estimated height in 1998, the year of the release thinning. In Douglas-fir, the 1998 height was estimated as the point five branch whorls below the top, excluding the

current-year growth. In western hemlock, the 1998 height was estimated by finding the point on the stem with branches that appeared to be 5 years old, based on annual changes in the color and texture of the bark. Height growth was calculated as the change in height in the 5-years 1998–2003, and relative height growth was the 5-year-height-growth increment divided by height in 1998.

The measured trees were harvested and two sections cut from each: a reference section (about 2 cm long, from near ground level), and a section for the determination of specific conductivity (about 15 cm long, from about 10 cm above ground level). The reference section was used in the field to measure bark thickness and to estimate the radius of heartwood and sapwood by painting them along perpendicular diameters with two sapwood/heartwood differentiation stains, alizarine red and methyl orange (Kutscha and Sachs 1962). None of the samples had heartwood, so sapwood area was calculated by measuring two diameters on the reference disk, taking the mean and calculating the area of a circle. Growth rings were counted to determine tree age.

*Leaf specific root conductance*

Immediately after harvesting the trees, we measured root conductance with a high-pressure flow meter (Tyree et al. 1995) and filtered tap water. Trees were cut with a handsaw, leaving about 5 cm of stump. The stump surface was recut with a razor blade. A tight-fitting rubber collar was placed around the stump and a plastic chamber was sealed to the top of the rubber collar. The water in the pressurized reservoir of the flow meter could then be forced to flow through one of six capillary tubes of varying size before flowing into the cut stump via the plastic chamber. The pressure at both ends of the chosen capillary tube was recorded and the flow rate (kg $s^{-1}$) was calculated from the difference in pressure across the capillary tube based on a predetermined regression equation for the relationship between the pressure difference and flow. The pressure head (MPa) driving water through the root system was defined as the pressure observed at the downstream end of the capillary tube. The temperature of a beaker of water located in close proximity to the high pressure flow meter was recorded so that a viscosity correction could be made. Root conductance ($k_R$) was calculated from Equation 1:

$$k_R = \frac{Q}{\Delta P} \quad (1)$$

where $Q$ is volume flow rate (kg $s^{-1}$) and $\Delta P$ is the pressure difference (MPa). We normalized $k_R$ by leaf area by dividing by the leaf area of the tree to give a measure of leaf specific root conductance ($k_{RL}$; kg $m^{-2}$ $s^{-1}$ $MPa^{-1}$).

*Leaf area*

As each tree was harvested, it was placed on a tarp and all branches with leaves were cut into sections about 10 cm long, which were weighed. Three random subsamples of the cut branches and leaves were oven dried at 50 °C for about 48 h, and their dry masses determined. We separated leaves from branches, reweighed the samples and calculated the ratio of leaf dry mass to leaf + branch dry mass.

About 20 to 30 fresh leaves were randomly selected from each tree, transported to the lab and frozen until their total area could be determined. The leaves were placed face down on the glass of the scanner along with an image of a reference square with an area of 1 $cm^2$. The leaves and the square were scanned and images imported into an image analysis system (Scion Image, version 4.0.2, Scion Corp., Frederick, MD) and leaf areas converted from pixels to $cm^2$. The samples of measured leaves were dried and leaf mass area (LMA; g $m^{-2}$) ratio (leaf dry mass:fresh leaf area) calculated. From the ratios of subsample leaf dry mass:leaf + branch dry mass, subsample leaf + branch fresh mass:leaf + branch dry mass, and fresh mass of all leaves and branches, we estimated fresh leaf area for the whole tree.

*Leaf specific conductivity*

Specific conductivity ($K_s$) values used in this study were from Renninger (2005). Briefly, two wood subsamples (1 cm × 1 cm × 10 cm, tangential × radial × longitudinal) were prepared from each 15-cm-long stem section. Subsamples included the outer growth ring, and usually two to three other rings interior to that in released trees and five to six rings in suppressed trees, depending on ring width. To the extent possible, we avoided compression wood and branch junctions in the samples. Samples were vacuum infiltrated with tap water for about 1 h, before $K_s$ was measured with a pressure sleeve apparatus (Spicer and Gartner 1998). Flow rate was corrected to 20 °C and $K_s$ calculated:

$$K_s = \frac{Ql}{A_{sample}\Delta P} \quad (2)$$

where $Q$ is volume flow rate (kg $s^{-1}$), $l$ is length of the sample (m), $A_{sample}$ is the cross-sectional area of the sample ($m^2$) and $\Delta P$ is the pressure difference between the two ends of the sample (MPa).

Leaf specific conductivity ($K_L$) was calculated as:

$$K_L = \frac{A_S}{A_L} K_s \quad (3)$$

where $A_S$ is sapwood area ($m^2$), $A_L$ is leaf area ($m^2$) and $K_s$ is specific conductivity (kg $m^{-1}$ $s^{-1}$ $MPa^{-1}$).

*Leaf water potential*

During August and September 2004, 24 trees (six trees per species at each site) were chosen from across the entire site to measure predawn and midday leaf water potentials. On three separate days, two branch samples from two trees of each species at each site were measured for predawn water potential with a pressure chamber (PMS, Corvallis, OR), and another two branch samples were measured for midday water potentials (1100 and 1200 h).

*Photosynthesis*

During a 2-week period in July 2005, light-response curves and $A/C_i$ curves were obtained for four trees of each species at each site. Curves were generated between 0900 and 1300 h with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE) equipped with a red/blue LED light source and a $CO_2$ injector. Leaf temperature matched air temperature closely and ranged from 20–30 °C.

Current-year leaves were measured on branches about 1 m above ground. Photosynthetically active radiation was determined at eight locations per site over a period of 2 weeks with a quantum sensor mounted horizontally on the cuvette during the $A/C_i$ curves determinations. To produce the light-response curves, $CO_2$ was held at a constant concentration of 400 μmol $mol^{-1}$ while PAR was progressively lowered from 1500 to 50 μmol $m^{-2}$ $s^{-1}$ in 200 μmol $m^{-2}$ $s^{-1}$ intervals. We graphed photosynthetically active radiation (PAR) versus assimilation rate (μmol $CO_2$ fixed $m^{-2}$ $s^{-1}$) individually for each tree as well as averaged over all trees in a given category. Graphs for individual trees were used to estimate quantum yield from the initial slope, light compensation point ($\tau$) from the $x$-intercept, dark respiration rate ($R_d$) from the $y$-intercept and maximum assimilation rate ($A_{max}$) at ambient [$CO_2$]. We recognize that quantum yield may be underestimated with this method (Singsaas et al. 2001); however, such error should not invalidate comparisons between species and across sites.

To obtain the $A/C_i$ curves, PAR was held at 1200 μmol $m^{-2}$ $s^{-1}$ while the cuvette $CO_2$ concentration was set, first near ambient (400 μmol $mol^{-1}$) and then lowered in 100 μmol $mol^{-1}$ intervals, finishing with a reading at 50 μmol $mol^{-1}$. Cuvette $CO_2$ concentration was then increased to 400 μmol $mol^{-1}$ and then in 200 μmol $mol^{-1}$ steps until no further increase in assimilation rate was elicited. Concentration of $CO_2$ inside the leaf ($C_i$) was plotted versus assimilation rate to construct $A/C_i$ curves for each tree and for all trees in a given category. Graphs from individual trees were used to estimate the $CO_2$ compensation point ($\Gamma$) from the $x$-intercept and $A_{max}$ at saturating [$CO_2$].

*$\delta^{13}C$ and leaf nitrogen concentration*

During late June 2004, we collected about 100 mg each of 1-, 2-, 3- and 4-year-old leaves from all sides and at all heights of five trees of each species. The 80 leaf samples were dried at 60 °C for at least 48 h, ground to a fine powder with a ball mill and analyzed for $\delta^{13}C$ and percent leaf nitrogen (N) at the University of Idaho Stable Isotopes Laboratory.

Standard deviations for the $CO_2$ and N standards ranged from 0.0001–0.0006. The amount of $^{13}C$ relative to $^{12}C$ in leaf tissue provides an indication of the intrinsic water-use efficiency (assimilation/stomatal conductance), and therefore relative stomatal limitation of photosynthesis, when the leaf was being formed (Farquhar et al. 1989). Leaf nitrogen was normalized by leaf area ($N_{area}$) based on leaf mass per area ratios for each category of foliage.

*Statistical analysis*

Although this study was pseudoreplicated (Hurlbert 1984), the results were evaluated by analysis of variance (ANOVA) as if it were truly replicated using individual trees as the experimental unit instead of site means. Although the trees were not randomly selected for analysis, selection on the basis of uniform height at the time of the 1998 thinning treatment should not have altered the patterns observed or conclusions drawn. Logistical constraints prevented the use of the same individuals for all types of measurements, but the tree selection criteria were chosen to avoid bias.

Means, 95% confidence intervals and $P$ values for comparisons of means were calculated for all variables in Tables 1 and 2 by PROC MIXED procedure in SAS version 9.1 (SAS Institute, Cary, NC). If needed, data were log-transformed to meet assumptions of normality and constant variance. Means and confidence intervals of the log-transformed data were back-transformed and reported on the original scale. Species and site were used as indicator variables and comparisons of means were made between each category. Differences in means were deemed significant if $P < 0.05$.

## Results

*Site conditions*

As expected, the thinned stand with its lower density of overstory trees received higher daily mean PAR in the understory compared with the unthinned stand (about 1400 versus 400 μmol $m^{-2}$ $s^{-1}$). In the unthinned stand, some light reached the understory vegetation as sun flecks. Nevertheless, PAR was much lower in the unthinned than in the thinned stand. Soil water potentials were similar in both stands as estimated by predawn water potential measurements on both species (Table 1).

*Relative height growth*

Current height of released Douglas-fir and western hemlock trees did not differ significantly nor did the current height of suppressed Douglas-fir and western hemlock trees (Table 1). However, height growth differed significantly among species and treatment groups. Suppressed western hemlock had 71% greater height growth than suppressed Douglas-fir, and released western hemlock had 19% greater height growth than released Douglas-fir. Relative height growth (height growth from 1998 to 2003/height in 1998) was significantly lower in Douglas-fir than in western hemlock in both released and suppressed trees (Table 1).

*Leaf specific root conductance*

Leaf specific root conductance ($k_{RL}$) did not differ significantly between released Douglas-fir and western hemlock (Table 1), but differed substantially between suppressed Douglas-fir and western hemlock. The value of $k_{RL}$ was 4.5 times larger in suppressed Douglas-fir than in released Douglas-fir, whereas $k_{RL}$ was not significantly different in suppressed and released western hemlock.

Table 1. Means and 95% confidence intervals for variables relating to hydraulic architecture in suppressed and released Douglas-fir and western hemlock trees. Within rows, different superscript letters signify a statistically significant difference ($P < 0.05$). Abbreviations: $K_s$ = specific conductivity; $k_{RL}$ = leaf-specific root conductivity; $A_L/A_S$ = leaf area:sapwood area ratio; $K_L$ = leaf-specific conductivity; and $\Psi$ = water potential.

| Variable | Douglas-fir | | Western hemlock | |
|---|---|---|---|---|
| | Suppressed | Released | Suppressed | Released |
| $K_s$[1] (kg m$^{-1}$ s$^{-1}$ MPa$^{-1}$) | 0.38 (0.28–0.51) a | 1.07 (0.80–1.45) b | 0.59 (0.44–0.80) a | 0.84 (0.62–1.13) b |
| Height (m) | 2.34 (1.99–2.68) a | 3.62 (3.28–4.00) b | 2.62 (2.28–2.97) a | 3.74 (3.39–4.08) b |
| Age (years) | 17.6 (15.8–19.4) a | 18.0 (16.2–19.8) a | 13.9 (12.1–15.7) b | 12.1 (10.3–13.9) b |
| Height growth (m) | 0.80 (0.54–1.07) a | 1.99 (1.73–2.25) b | 1.37 (1.11–1.63) c | 2.36 (2.10–2.63) d |
| Relative height growth (m m$^{-1}$) | 0.51 (0.419–0.625) a | 1.22 (0.998–1.49) b | 1.03 (0.84–1.25) b | 1.74 (1.42–2.12) c |
| $k_{RL} \times 10^{-4}$ (kg m$^{-2}$ s$^{-1}$ MPa$^{-1}$) | 4.51(2.53–8.02) a | 1.00 (0.54–1.83) b | 1.47 (0.82–2.61) b | 1.04 (0.52–2.07) b |
| Leaf area (m$^2$) | 0.69 (0.54–0.89) a | 9.77 (7.59–12.56) b | 2.07 (1.61–2.66) c | 9.90 (7.70–12.74) b |
| Sapwood area $\times 10^{-4}$ (m$^2$) | 2.57 (2.1–3.1) a | 9.79 (8.1–11.8) b | 3.35 (2.8–4.0) a | 10.95 (9.1–13.2) b |
| $A_L/A_S$ (m$^2$ cm$^{-2}$) | 0.27 (0.23–0.31) a | 1.00 (0.87–1.14) b | 0.62 (0.54–0.71) c | 0.90 (0.79–1.03) b |
| $K_L \times 10^{-4}$ (kg m$^{-1}$ s$^{-1}$ MPa$^{-1}$) | 1.48 (1.15–1.81) a | 1.16 (0.83–1.50) a | 1.06 (0.73–1.39) a | 1.09 (0.75–1.42) a |
| Predawn $\Psi$ (MPa) | −0.53 (−0.43 to −0.63) a | −0.54 (−0.43 to −0.64) a | −0.34 (−0.24 to −0.45) b | −0.35 (−0.25 to −0.46) b |
| Midday $\Psi$ (MPa) | −1.22 (−1.09 to −1.35) a | −1.28 (−1.16 to −1.41) a | −1.16 (−1.03 to −1.28) ab | −1.07 (−0.95 to −1.20) b |

[1] Values taken from Renninger 2005.

*Aboveground hydraulic architecture*

Released Douglas-fir had 14 times more leaf area than suppressed Douglas-fir, whereas released western hemlock had about five times more leaf area than suppressed western hemlock (Table 1). Differences in sapwood area were less pronounced. Released Douglas-fir had 3.8 times the sapwood area of suppressed Douglas-fir, whereas released western hemlock had almost 3.3 times the sapwood area of suppressed western hemlock (Table 1).

Leaf area:sapwood area ratios ($A_L/A_S$) differed significantly between suppressed and released trees, and the differences were greater in Douglas-fir than in western hemlock. In released Douglas-fir, $A_L/A_S$ was 3.7 times larger than in suppressed Douglas-fir, whereas $A_L/A_S$ in released western hemlock was only 1.45 times greater than in suppressed western hemlock (Table 1).

The relationship between relative height growth and $A_L/A_S$ was not significant in suppressed Douglas-fir, whereas relative height growth decreased slightly as $A_L/A_S$ increased in released Douglas-fir ($r^2 = 0.2$, $P = 0.036$; Figure 1). The relationship between relative height growth and $A_L/A_S$ was not significant for released western hemlock, whereas relative height growth decreased sharply as $A_L/A_S$ increased in suppressed western hemlock ($r^2 = 0.6$, $P = 0.009$).

Despite differences in leaf area, sapwood area and $K_s$, leaf-specific conductivities ($K_L$) did not differ significantly ($P = 0.183$) between suppressed and released trees of either Douglas-fir or western hemlock.

*Leaf water potentials*

Both Douglas-fir and western hemlock had similar midday water potentials whether suppressed or released (Table 1).

*Photosynthesis*

Mean values of $N_{area}$ were 48% higher in released Douglas-fir than in suppressed Douglas-fir, whereas released western hemlock needles had 29% more nitrogen than suppressed western hemlock needles (Table 2). Suppressed Douglas-fir had a mean $N_{area}$ 59% greater than suppressed western hemlock, but one third of the leaf area, whereas released Douglas-fir had a mean $N_{area}$ 83% greater than released western hemlock and about the same leaf area (Table 2). In suppressed and released Douglas-fir, needle age had no significant effect on $N_{area}$ (Figure 2). However, in suppressed and released western hemlock, $N_{area}$ decreased with increasing needle age ($P < 0.0001$ and 0.008, respectively; Figure 2).

Light-response curves for suppressed and released trees were consistent with the differences in light environment (Figure 3). Values of $A_{max}$ differed significantly between sup-

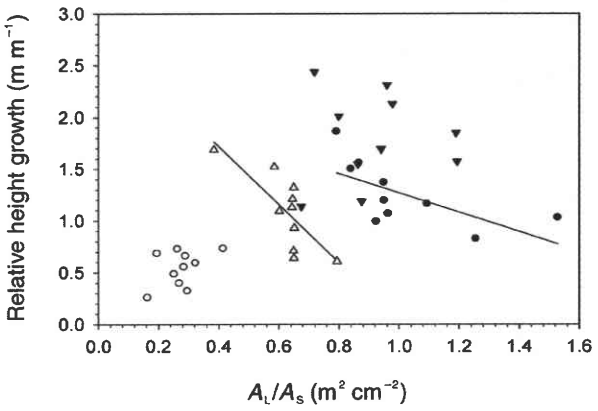


Figure 1. Relationship between relative height growth and leaf area:sapwood area ratio ($A_L/A_S$) in suppressed and released understory trees. Relationships between species/site categories differed, so separate regressions were made for each and only significant regressions are shown. Symbols: ●, ○ = Douglas-fir; △, ▼ = western hemlock; open symbols = suppressed trees; and closed symbols = released trees.

Table 2. Means and 95% confidence intervals for variables relating to photosynthesis in suppressed and released Douglas-fir and western hemlock trees. Within rows, different superscript letters signify a statistically significant difference ($P < 0.05$). Abbreviations: $N_{area}$ = leaf nitrogen concentration; $A_{max}$ = maximum assimilation rate; and LMA = leaf dry mass:fresh leaf area ratio.

| Variable | Douglas-fir | | Western hemlock | |
|---|---|---|---|---|
| | Suppressed | Released | Suppressed | Released |
| $N_{area}$ (mmol N $m^{-2}$) | 87.6 (82.3–92.8) a | 129.9 (124.6–135.1) b | 55.2 (49.9–60.5) d | 71.0 (65.7–76.3) c |
| Quantum yield (μmol $CO_2$ μmol $PAR^{-1}$) | 0.015 (0.011–0.018) ac | 0.018 (0.015–0.021) a | 0.015 (0.011–0.019) a | 0.020 (0.016–0.023) c |
| Light compensation point (τ; μmol $m^{-2}$ $s^{-1}$) | 49 (41–58) a | 47 (36–59)a | 33 (24–43) b | 42 (32–51) ab |
| Dark respiration rate ($R_d$; μmol $m^{-2}$ $s^{-1}$) | −0.7 (−0.9 to −0.6) ab | −1.0 (−1.2 to −0.7) a | −0.5 (−0.7 to −0.3) b | −0.8 (−1.0 to −0.6) a |
| $A_{max}$ (ambient $CO_2$; μmol $m^{-2}$ $s^{-1}$) | 1.6 (1.0–2.3) a | 2.6 (2.0–3.2) b | 1.5 (0.8–2.2) a | 3.1 (2.4–3.8) b |
| $A_{max}$ (saturating $CO_2$; μmol $m^{-2}$ $s^{-1}$) | 4.1 (2.9–5.3) a | 9.7 (8.6–10.9) b | 4.9 (3.7–6.0) a | 8.2 (7.1–9.4) c |
| $CO_2$ compensation point (Γ; μmol $m^{-2}$ $s^{-1}$) | 20 (7–54) a | 28 (14–55) a | 38 (22–68) a | 23 (13–41) a |
| $\delta^{13}C$ (‰) | −31.78 | −30.56 | −31.62 | −30.97 |
| (range) | (−32.27 to −31.28) a | (−31.06 to−30.07) b | (−32.11 to −31.13) a | (−31.47 to −30.48) b |
| LMA (g $m^{-2}$) | 146.0 (106.1–201.0) a | 65.2 (47.4–89.8) b | 103.0 (74.8–141.7) ac | 73.9 (53.7–101.7) bc |

pressed and released trees, although differences between species were not significant (Table 2). For Douglas-fir and western hemlock, $A_{max}$ was 55% and about 100% higher, respectively, in released trees than in suppressed trees. Released western hemlock had a 21% higher $A_{max}$ than released Douglas-fir; however, this difference was not significant. Dark respiration rates ($R_d$) did not differ significantly between suppressed and released Douglas-fir trees, but they differed significantly between suppressed and released western hemlock trees (Table 2). Released western hemlock trees had 66% higher $R_d$ than suppressed trees. Although released western hemlock showed no photoinhibition at the highest irradiances, released Douglas-fir showed slight photoinhibition at the highest irradiance. Suppressed trees of both species showed some photoinhibition, which was more pronounced in western hemlock than in Douglas-fir. Additionally, there was a significantly positive relationship between relative height growth and $A_{max}$ at saturating light and ambient [$CO_2$] ($r^2 = 0.40$, $P = 0.0032$; Figure 4).

Although released western hemlock had higher assimilation rates when light was increased and [$CO_2$] was held constant, a different pattern emerged when irradiance was held constant and [$CO_2$] was increased. Released Douglas-fir had 18% higher $A_{max}$ at saturating [$CO_2$] than released western hemlock (Table 2; Figure 5). Additionally, $A_{max}$ at saturating [$CO_2$] was 2.4 times higher for released than for suppressed Douglas-fir, whereas $A_{max}$ at saturating [$CO_2$] was 1.7 times higher for re-

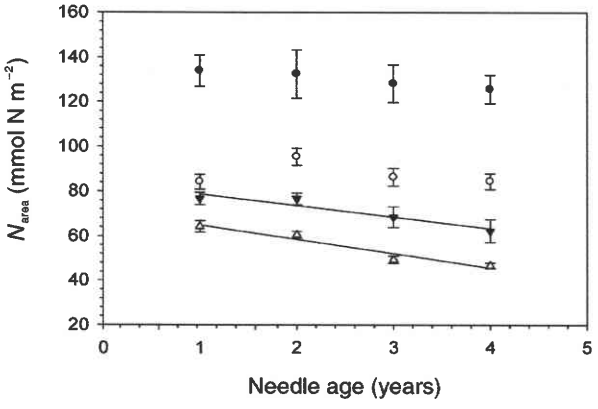


Figure 2. Relationship between leaf nitrogen concentration ($N_{area}$) and needle age in suppressed (open symbols) and released (closed symbols) Douglas-fir (●, ○) and western hemlock (▼, △). Only significant regressions are shown, and $r^2$ for suppressed and released western hemlock were 0.94 and 0.90, respectively.

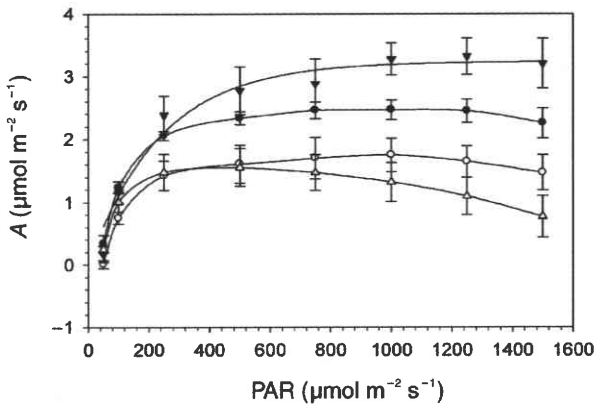


Figure 3. Light response curves for suppressed and released Douglas-fir and western hemlock trees. Symbols: ●, ○ = Douglas-fir; ▼, △ = western hemlock; open symbols = suppressed trees; and closed symbols = released trees.

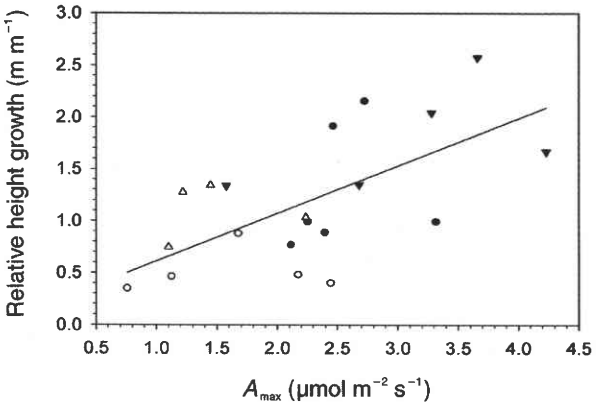


Figure 4. Relationship between relative height growth and maximum assimilation rate ($A_{max}$) at ambient [$CO_2$]. Symbols: ●, ○ = Douglas-fir; ▼, △ = western hemlock; open symbols = suppressed trees; and closed symbols = released trees.

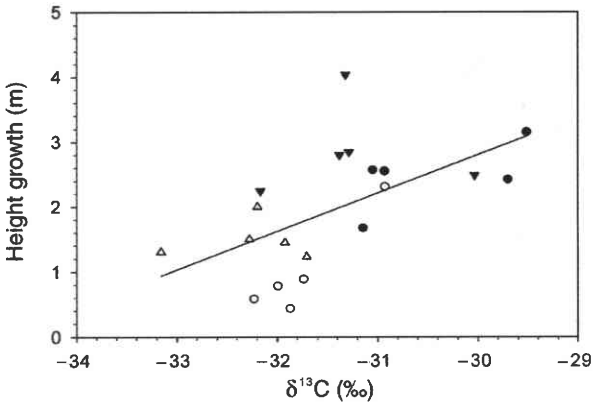


Figure 6. Relationship between absolute height growth and mean $\delta^{13}C$ of the four foliar age classes. Symbols: ●, ○ = Douglas-fir; ▼, △ = western hemlock; open symbols = suppressed trees; and closed symbols = released trees.

leased than suppressed western hemlock (Table 2). Both suppressed Douglas-fir and western hemlock had similar assimilation rates at any given internal [$CO_2$]. All $A/C_i$ curves yielded similar estimates of $CO_2$ compensation points.

### $\delta^{13}C$

In both species, foliar $\delta^{13}C$ was significantly less negative in released trees than in suppressed trees (Table 2). Foliar $\delta^{13}C$ values were positively correlated with height growth ($r^2$ = 0.33, $P$ = 0.0086; Figure 6). Height growth increased as mean $\delta^{13}C$ for the four foliar age classes became less negative (more enriched). As $A_L/A_S$ increased, $\delta^{13}C$ of 1-year-old foliage became linearly less negative ($r^2$ = 0.49, $P$ = 0.01; Figure 7).

## Discussion

Although relative height growth in released western hemlock was greater than in released Douglas-fir, the difference in relative height growth between suppressed and released trees was greater in Douglas-fir than in western hemlock. The lower relative growth of suppressed Douglas-fir compared with suppressed western hemlock indicates that Douglas-fir trees were more severely suppressed in shade and, therefore, more responsive to release. Consistent with these results, Tesch and Korpela (1993) found that mean annual height growth of Douglas-fir almost doubled five years after release and continued to increase as the trees adjusted to their new environment.

One reason for the perceived lack of response of Douglas-fir to release treatments is that the response is delayed relative to the response of species like western hemlock. The delayed response to release in Douglas-fir compared with western hemlock may result from differences in growth patterns. Growth of western hemlock is indeterminate, whereas growth of Douglas-fir is determinate, meaning that shoot growth depends to a

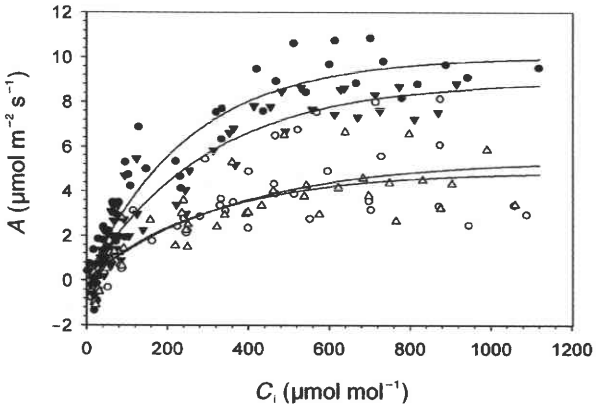


Figure 5. The $A/C_i$ curves for suppressed and released Douglas-fir and western hemlock trees. Symbols: ●, ○ = Douglas-fir; ▼, △ = western hemlock; open symbols = suppressed trees; and closed symbols = released trees.

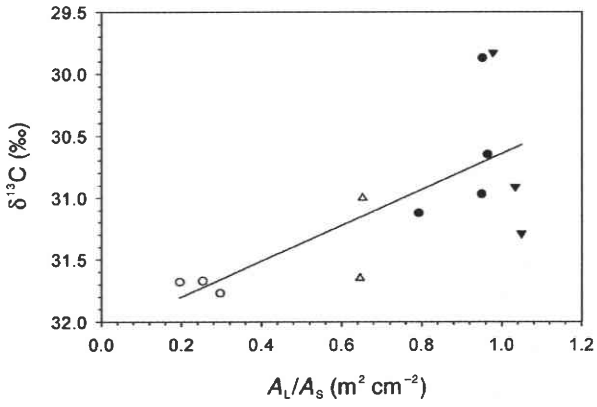


Figure 7. Relationship between leaf area:sapwood area ratio ($A_L/A_S$) and $\delta^{13}C$ of the 1-year-old foliage. Symbols: ●, ○ = Douglas-fir; ▼, △ = western hemlock; open symbols = suppressed trees; and closed symbols = released trees.

larger extent on the amount of cell division that occurred in the bud during the previous year (Cannell et al. 1976, Kneeshaw et al. 2002). This is further illustrated by a study reporting that the previous year's competition explained 65% of current-year shoot growth in Douglas-fir, whereas the current year's competition explained only 6% of shoot growth (Harrington and Tappeiner 1991). Therefore, Douglas-fir may not show increases in growth rate the year after release because its buds were formed under conditions causing suppression in the previous year.

Our observations indicate that both hydraulic architecture and photosynthetic capacity constrained release from suppression in Douglas-fir and western hemlock. It appeared that photosynthetic capacity was the larger constraint initially, and that hydraulic architecture became a constraint later on. Initially, both species increased dry mass allocation to leaf tissue and thus increased their photosynthetic capacity. This shift increased the leaf area of trees relative to sapwood area, which likely caused hydraulic architecture to limit increased carbon gain. Released trees had a substantially greater $N_{area}$ than suppressed trees and, in turn, higher $A_{max}$ at saturating [$CO_2$] than suppressed trees, suggesting that released trees needed to construct needles with greater photosynthetic capacity after release from suppression. Released western hemlock trees produced needles acclimated to the higher PAR following overstory thinning and did not exhibit photoinhibition as observed in needles of suppressed western hemlock (Figure 3).

Several lines of evidence led to the conclusion that hydraulic architecture limited carbon gain after release from suppression to a greater extent in Douglas-fir than in western hemlock. First, there were differences in leaf specific root conductance ($k_{RL}$) between suppressed and released trees. In Douglas-fir, $k_{RL}$ was 4.5 times larger and $K_L$ was 1.3 times larger (although the difference was not significant at $P < 0.05$) in suppressed trees than in released trees. In western hemlock, $k_{RL}$ and $K_L$ did not differ significantly between suppressed and released trees. Growth rings became wider, tracheids became longer and wider, earlywood proportion became higher, and consequently, wood density became slightly lower in the released trees, facilitating increases in specific conductivity and $K_L$ (Renninger 2005). Because the root system and tree stem are in series, their resistances to water flow can be considered additive. Although both species had lower whole-tree conductances after release than before, the difference was greatest in Douglas-fir. Hubbard et al. (2001) found that, if trees maintain a constant minimum midday water potential, reductions in $K_L$ (and presumably $k_{RL}$) cause stomatal conductance to decrease and, in turn, assimilation to decline. In our study, photosynthetic capacity increased and whole-plant leaf specific conductance decreased following release, whereas minimum leaf water potentials remained constant. Stomatal restriction of transpiration to maintain constant minimum leaf water potential despite reduced leaf specific hydraulic conductance therefore led to increased relative stomatal limitation of photosynthesis in released trees. Douglas-fir probably experienced more hydraulic limitation after release from suppression than western hemlock because of the greater differences in this species in $K_L$ and $k_{RL}$ between suppressed and released trees.

The second piece of evidence that hydraulic architecture limited release in Douglas-fir was the relationship between relative height growth and $A_L/A_S$. There was no relationship between relative height growth and $A_L/A_S$ for either suppressed Douglas-fir or released western hemlock (Figure 1). However, in released Douglas-fir and suppressed western hemlock, relative height growth decreased as $A_L/A_S$ increased, suggesting that relative height growth in released Douglas-fir (and suppressed western hemlock) was constrained by stomatal closure and trees exhibited greater relative height growth when they had less leaf area that needed to be supplied with water for a given amount of sapwood area. Additionally, leaves became more enriched in $^{13}C$ as $A_L/A_S$ increased, suggesting a greater stomatal limitation on photosynthesis as a greater leaf area needed to be supplied by a given sapwood area (Figure 7). Although uptake of $CO_2$ respired from the soil could have affected $\delta^{13}C$ values in our understory trees, the trees at each site should have been exposed to about the same $CO_2$ pool.

A third piece of evidence that hydraulic architecture limited release to a greater extent in Douglas-fir than in western hemlock relates to differences in $A_{max}$ estimated from the light-response curves and the $A/C_i$ curves. For both species, $A_{max}$ observed at saturating [$CO_2$] was significantly higher than when PAR was increased and [$CO_2$] was held constant at the ambient value. However, the ratio of $A_{max}$ at saturating [$CO_2$] to $A_{max}$ at ambient [$CO_2$] in Douglas-fir increased from 2.5 in suppressed trees to 3.8 in released trees, whereas in western hemlock this ratio decreased from 3.2 in suppressed trees to 2.7 in released trees. These results imply that, following release, relative stomatal limitation on carbon gain increased in Douglas-fir and decreased in western hemlock. This interpretation is consistent with the relationships between relative height growth and $A_L/A_S$ showing that both released Douglas-fir and suppressed western hemlock exhibited decreased relative height growth with increased $A_L/A_S$ and presumably increased stomatal limitation on carbon gain.

Although released Douglas-fir needles had 83% more $N_{area}$ than released western hemlock needles, they had slightly lower $A_{max}$ at ambient [$CO_2$]. These findings again lead to the conclusion that released Douglas-fir trees were unable to take full advantage of their increased photosynthetic capacity associated with increased nitrogen concentration because photosynthesis was stomatally limited. Likewise, trees with greater height growth exhibited less negative $\delta^{13}C$ values implying that the increases in photosynthetic capacity were greater than the ability of the tree to supply water to the needles causing a stomatal limitation on assimilation.

Our comparison of the abilities of Douglas-fir and western hemlock to release revealed differences in species plasticity. Douglas-fir showed greater plasticity in hydraulic architecture than western hemlock. It is commonly thought that plasticity is positively related to the degree of shade tolerance of a species. Douglas-fir tended to show much more variation in $A_L/A_S$, $k_{RL}$ and $K_L$ than western hemlock in that these parameters varied substantially depending on the environment in which the trees

were growing. However, western hemlock showed more plasticity than Douglas-fir in leaf functional traits. For example, western hemlock appeared to reallocate nitrogen from older needles to younger needles (Figure 2), which may furnish it with an advantage over Douglas-fir during release. Brooks et al. (1996) also found that foliar N concentration in *Abies amabilis* (Dougl. ex Forbes) decreased with increased shading. Although there are costs associated with nitrogen redistribution, in the long run these costs are reported to be smaller than the benefits of redistributing nitrogen to better lit leaves (Field 1983). In western hemlock, quantum yield, $R_d$ and $A_{max}$ differed significantly between suppressed and released trees, whereas in Douglas-fir only $A_{max}$ differed significantly. Douglas-fir appeared to lack the ability to produce shade-adapted leaves, but reduced its leaf area in shade, thereby reducing leaf maintenance respiration.

Although suppressed Douglas-fir responded to release, hydraulic architecture and photosynthetic capacity initially constrained the response, possibly at different periods after thinning. However, our research was conducted on one site in the relatively humid, central Oregon Coast Range on only one age class of trees, and therefore, these results may be inapplicable to sites where drier conditions prevail. Our data were collected 6 years following the release thinning, and so the sequence of changes occurring during release are speculative. Information on the constraint immediately following release could provide guidance on how best to achieve the most rapid release of suppressed trees. For example, because photosynthetic capacity appeared initially to constrain release, initial release thinnings could be light to avoid photoinhibition and increased stress suppression on trees. After photosynthetic capacity has increased, more intense thinnings could be performed to achieve further release. Because released western hemlock had greater height growth than released Douglas-fir, thinning of the western hemlock advance regeneration may be needed in the future to ensure that released Douglas-fir is not overtopped, thereby maintaining a mix of tree species that is often desired in uneven-aged stands.

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