

Effects of release from suppression on wood functional characteristics in young Douglas-fir and western hemlock

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Abstract: Little is known of wood properties in trees that were initially suppressed and subsequently released from suppression. The purpose of this study was to assess differences in growth ring width, specific conductivity (K_s), tracheid dimensions, moisture content, and wood density in suppressed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees and trees released from suppression averaging 12–18 years of age. Growth ring width was 370% higher for Douglas-fir and 300% higher for western hemlock trees released from suppression, and K_s was 182% higher for Douglas-fir and 42% higher for western hemlock trees released from suppression. Earlywood width was approximately four times greater after release in both species, whereas the relative increase in latewood width was much greater in Douglas-fir. Tracheids were 25% wider and 11% longer in released Douglas-fir trees. In western hemlock, released trees had 19% wider tracheids that were approximately the same length as those in suppressed trees. Moisture content was 66% greater in released Douglas-fir and 41% greater in released western hemlock. Wood density decreased by 21% in Douglas-fir trees and by 11% in western hemlock trees released from suppression. However, wood density of released trees did not differ from average reported values, implying that wood from released trees may be suitable for many of its traditional applications.

Résumé : On connaît peu de choses des propriétés du bois dans les arbres initialement supprimés et dégagés par la suite. Le but de cette étude consistait à évaluer les différences dans la largeur des cernes annuels, la conductivité spécifique (K_s), la dimension des trachéides, le contenu en eau et la densité du bois entre des tiges supprimées et des tiges dégagées de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) ainsi que de pruche occidentale (*Tsuga heterophylla* (Raf.) Sarg.) ayant en moyenne 12–18 ans. La largeur des cernes annuels était 370 % plus grande chez les tiges de douglas de Menzies et 300 % plus grande chez les tiges de pruche occidentale dégagées et K_s était 182 % plus élevée chez les tiges de douglas de Menzies et 42 % plus élevée chez les tiges de pruche occidentale qui avaient été dégagées. La largeur du bois initial était approximativement quatre fois plus grande après le dégagement chez les deux espèces tandis que l'augmentation relative de la largeur du bois final était beaucoup plus forte chez le douglas de Menzies. Les trachéides étaient 25 % plus larges et 11 % plus longues chez les tiges dégagées de douglas de Menzies. Chez la pruche occidentale, les trachéides des tiges dégagées étaient 19 % plus larges et avaient approximativement la même longueur que chez les tiges supprimées. Le contenu en eau des tiges dégagées était 66 % plus élevé chez le douglas de Menzies et 41 % plus élevé chez la pruche occidentale. La densité du bois des tiges dégagées a diminué de 21 % chez le douglas de Menzies et de 11 % chez la pruche occidentale. Cependant, la densité du bois des tiges dégagées ne différait pas des valeurs moyenne déjà rapportées, ce qui implique que le bois des tiges dégagées peut convenir à plusieurs des usages traditionnels.

[Traduit par la Rédaction]

Introduction

Forestry practices in the Pacific Northwest are beginning to shift from even-aged to uneven-aged stand management, and therefore, the regeneration that will replace these stands is changing (O'Hara 2001). Regeneration in uneven-aged

stands comes from saplings that were suppressed under the canopy of mature trees. Through selection thinnings that remove selected mature trees with the purpose of opening up the canopy, these saplings can be released from suppression and grow to become a part of the overstory (Miller and Emmingham 2001). Trees that have spent the beginning of

Received 31 October 2005 Accepted 18 April 2006. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 1 August 2006.

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their lives suppressed in the understory may also make better crop trees (from a wood-quality perspective) compared with seedlings that are grown in open conditions because their core of juvenile wood and branch size on the first log are likely to be smaller (Cregg et al. 1988; Watson et al. 2003).

Additionally, trees that are suppressed during the beginning of their lives exhibit recession of their crown earlier than trees growing in open conditions. Therefore, changes in crown architecture caused by periods of suppression could also change wood properties. For example, Larson (1969) found in red pine (*Pinus resinosa* Soland.) that tracheid diameter and percent earlywood were higher and cell walls thinner in stemwood formed within the crown than in wood formed below the crown. Also, crown length and branch longevity affect the location and size of knots. Because suppressed trees have been growing slowly, they exhibit tight growth rings, small knots, and straight stems making them suitable for use in value-added products (LeVan-Green and Livingston 2001). Green et al. (2005) found that 70- to 90-year-old suppressed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) had very good grade recovery with 68% qualifying for select structural lumber.

It is usually assumed that seedlings growing in the understory are suppressed, even though it is likely that they first germinated in understory gaps (Spies et al. 1990). The patterns of wood development in open- and plantation-grown trees are generally well characterized (e.g., Zobel and van Buijtenen 1989; DeBell et al. 2004), but the properties of shade-grown, suppressed trees could be different. For example, age-related changes in growth ring width, earlywood width, and latewood width were much less dramatic in suppressed Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) than in dominant trees in the same age ranges (Fabris 2000).

Although few studies have examined wood anatomy in saplings released from suppression, perhaps insight can be gained by characterizing the changes that occur when trees are released by a thinning treatment. In fast-growing spruces, Dutilleul et al. (1998) found negative correlations between ring width and fiber length and between ring width and wood density, especially in juvenile wood. Zahner and Oliver (1962) also found that thinning delayed the transition from earlywood (less dense) to latewood (more dense) by about 2 to 3 weeks in red pine and jack pine (*Pinus banksiana* Lamb.), implying that wood produced in these growth rings could have a decreased density. However, Markstrom et al. (1983) found that, although radial growth increased in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) after thinning, wood density, latewood percentage, tracheid length, and microfibril angle were not significantly different. Additionally, thinning of a Norway spruce (*Picea abies* (L.) Karst.) stand had little effect on wood density (Jaakkola et al. 2005a) but resulted in slightly shorter tracheids (Jaakkola et al. 2005b). Therefore, there is some uncertainty with regard to the changes in wood properties that will occur in trees that are released from suppression.

One would expect changes in the wood because trees tend to balance their leaf area with the area and permeability of their sapwood (Margolis et al. 1988). We already reported that these released trees had much greater leaf area, photosynthetic capacity, and leaf area:sapwood area ratios (A_L/A_S)

than suppressed trees (Renninger et al. 2006) (Table 1), both of which should create a higher demand for water transport, which in turn could be associated with changes in stem wood properties. Trees could increase their water transport capacity by any of the following changes: increasing sapwood area by increasing new growth ring width and (or) by decreasing the rate at which sapwood is changed to heartwood, or by changing the anatomical features of the wood produced to make it more conductive, i.e., increase specific conductivity (K_s) (Ewers 1985). Trees could potentially produce less dense wood after suppression for two reasons: to make a greater volume increment of wood in the form of wider growth rings, they may be constrained to make "cheaper wood" that is not as dense as that made previously; to make more conductive wood, they may need to make wood that has a lower latewood proportion (Domec and Gartner 2002) and, thus, is less dense. Because of the great importance of wood density and uniformity in wood utilization, changes in silviculture could affect the suitability of wood for various uses. However, in species like Douglas-fir that exhibit strong pith to bark trends in density, trees released from suppression may actually have wood that is more uniform in wood density and, therefore, better suited for certain applications.

This study addresses the changes in wood anatomy that are most closely associated with release from suppression. Douglas-fir and western hemlock were compared because they are commercially important species in the Pacific Northwest and have differing levels of shade tolerance (with western hemlock being more shade tolerant than Douglas-fir; Minore 1979), which could lead to contrasting responses upon release. We already reported that suppressed trees were shorter than released trees in both Douglas-fir and western hemlock (Renninger et al. 2006; see Table 1) and that height growth in the most recent 5-year period was lowest in suppressed Douglas-fir trees, followed by suppressed western hemlock, released Douglas-fir, and then released western hemlock. Our interpretation of these data along with data on hydraulic architecture was that both species showed release from suppression. Both species appeared to be initially constrained by photosynthetic capacity then, as leaf area increased, became constrained by hydraulic architecture; this was more apparent for Douglas-fir than for western hemlock.

In this study, we wished to determine how specific wood properties changed in young Douglas-fir and western hemlock in response to release from suppression. In particular, the first research question addressed whether Douglas-fir and western hemlock responded more strongly to release from suppression with increases in growth ring width or increases in K_s . We hypothesized that trees released from suppression would increase the width of their growth rings as well as the proportion of earlywood to latewood within individual growth rings. Furthermore, trees released from suppression should produce more conductive wood with higher K_s through the production of tracheids that are longer and have larger diameters. In our second research question, we asked how wood density is affected after trees release from suppression. We hypothesized that wood density would decrease in trees released from suppression because of decreased latewood proportion and increases in tracheid diameter.

Table 1. Morphological, anatomical, and physiological characteristics in suppressed versus released trees of Douglas-fir and western hemlock.

Characteristic	Douglas-fir		Western hemlock	
	Suppressed	Released	Suppressed	Released
Leaf area (m ²)*	0.69a (0.54–0.89)	9.77b (7.59–12.56)	2.07c (1.61–2.66)	9.90b (7.70–12.74)
A _L /A _S (m ² cm ⁻²)*	0.27a (0.23–0.31)	1.00b (0.87–1.14)	0.62c (0.54–0.71)	0.90b (0.79–1.03)
Height (m)*	2.34a (1.99–2.68)	3.62b (3.28–4.00)	2.62a (2.28–2.97)	3.74b (3.39–4.08)
Height growth (m)*	0.80a (0.54–1.07)	1.99b (1.73–2.25)	1.37c (1.11–1.63)	2.36d (2.10–2.63)
Age (years)*	17.6a (15.8–19.4)	18.0a (16.2–19.8)	13.9b (12.1–15.7)	12.1b (10.3–13.9)
Growth ring width (mm)	0.54a (0.45–0.64)	1.99b (1.68–2.35)	0.94c (0.79–1.11)	2.91d (2.46–3.44)
Earlywood width (mm)	0.31a (0.26–0.38)	1.32b (1.08–1.61)	0.65c (0.54–0.80)	2.46d (2.02–3.00)
Latewood width (mm)	0.22a (0.18–0.27)	0.65b (0.53–0.80)	0.26a (0.21–0.32)	0.41c (0.33–0.50)
Percent latewood (%)	43.2a (38.4–47.9)	34.0b (29.3–38.7)	30.0b (25.1–34.6)	15.9c (11.2–20.6)
K _s (kg·m ⁻¹ ·s ⁻¹ ·GPa ⁻¹)	0.38a (0.28–0.51)	1.07b (0.80–1.45)	0.59a (0.44–0.80)	0.84b (0.62–1.13)
Tracheid diameter (mm)	24.3a (22.8–25.7)	30.4b (28.9–31.9)	22.7a (21.2–24.2)	27.1c (25.6–28.5)
Tracheid length (mm)	1.69a (1.61–1.77)	1.87b (1.79–1.96)	1.75a (1.67–1.83)	1.64a (1.56–1.72)
Wood density (g·cm ⁻³)	0.57a (0.55–0.59)	0.47b (0.45–0.49)	0.50c (0.49–0.52)	0.45b (0.44–0.47)
Moisture content (%)	66.5a (55.5–77.6)	110.3b (99.2–121.3)	96.6b (85.5–107.6)	136.2c (125.2–147.3)
Relative water content (%)	0.60a (0.54–0.67)	0.75b (0.68–0.82)	0.73b (0.66–0.80)	0.87c (0.80–0.94)

Note: Values are means with 95% confidence intervals given in parentheses. Means within a row with different letters are significantly different ($p < 0.05$).

*Values taken from Renninger et al. (2006).

Materials and methods

Site description

The approximately 30 ha site for this study was located in the Coast Range near Falls City, Oregon (44.82°N, 123.62°W, elevation 350 m), and had a site index at age 50 years of 128. The site was thinned from 415 trees/ha to 289 trees/ha in 1978 to allow self-seeding of Douglas-fir and western hemlock that were to function as advance regeneration. In 1998, a portion of the site (approximately 20 ha) was thinned again to a density of 99–148 trees/ha, which released the Douglas-fir and western hemlock advance regeneration from suppression. An adjacent portion of the site (approximately 10 ha) remained unthinned and contained Douglas-fir and western hemlock trees still suppressed in the understory. 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 harvest

In June and July 2004, we nonrandomly chose 10 trees of each species (Douglas-fir and western hemlock) in each site (suppressed and released). We chose trees that we estimated to be 1–2 m tall in 1998, exhibited no signs of damage to the bark, had no branches strongly competing with the terminal shoot for dominance, and were distributed across the entire range of the sites. These trees averaged 12–18 years, depending on species and treatment. Height and height growth since 1998 for these trees have been reported previously by Renninger et al. (2006) (Table 1). Briefly, in Douglas-fir, the 1998 height was estimated as the point five branch whorls below the top, not including the current year's growth. In

western hemlock, the 1998 height was estimated by finding the point on the stem that had branches that appeared to be 5 years old based on annual changes in the color and texture of their bark. Height growth was calculated as the change in height in the 5-year period from 1998 to 2003.

After the height was measured, we harvested trees and took two disks for this study: a disk for moisture content (about 2 cm long, from about 5 cm above ground level) and a disk for specific conductivity (about 15 cm long, from about 10 cm above ground level). In the field, we removed the bark from the moisture content disks then obtained fresh mass (M_f). Both the moisture content disks and the specific conductivity disks were placed in a plastic bag with wet paper towels and then transported to the laboratory within several hours.

Sapwood area, age, and tree leaf area were also estimated and have been described previously by Renninger et al. (2006) (Table 1). Briefly, we estimated sapwood area by painting two sapwood–heartwood differentiation stains, along two perpendicular diameters of our disks (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 average, and calculating the area of a circle. Additionally, growth rings were counted to determine age of the trees. To determine leaf area, all branches containing leaves were cut into pieces approximately 10 cm long. The mass of the fresh branches and leaves was obtained. Next, three random subsamples from each tree were weighed and dried. We separated leaves from branches, reweighed samples, and calculated the ratio of dry leaf mass to dry leaf and branch mass. Additionally, approximately 20–30 fresh leaves were randomly selected, their area was determined using a scanner and they were dried and weighed. Using the ratio of subsample leaf dry mass to leaf and branch dry mass, the ratio of the subsample of fresh mass of leaves and branches

to dry mass of leaves and branches, and the fresh mass of all leaves and branches, we were able to estimate fresh leaf area for the whole tree.

Specific conductivity

Upon return from the field site, specific conductivity samples were submerged in water and placed in a cold room (5 °C) until they could be processed the next morning. We prepared two subsamples (1 cm × 1 cm in cross-section × 10 cm long) from each sample. Subsamples were first cut roughly to size using a band saw and were then refined to their final size using a chisel making sure to follow the grain along the length of the sample. Samples included the outer growth ring and, usually, two or three other rings interior to that in released trees and five or six rings in suppressed trees, depending on ring width. To the extent possible, we avoided compression wood and branch junctions in the samples. After the samples were cut to their final dimensions, they were vacuum infiltrated in tap water for approximately 1 h.

Specific conductivity was measured using a pressure sleeve apparatus where the sample is placed in a chamber containing a latex membrane (Spicer and Gartner 1998). A very low pressure was applied to the chamber to press the membrane against the sample to prevent water leakage from its cut sides. For flow measurements, filtered water at pH 2 was placed in an Erlenmeyer flask at a height of 0.48 m above the sample creating a pressure head of 0.0048 MPa. Tubing was connected from the flask to the upstream end of the sample. Tubing also connected the downstream end of the sample to a pipette, marked in graduations of 0.01 mL. The time required for the meniscus to pass consecutive units of 0.05 mL was tracked using a stopwatch making certain that a fairly constant rate was achieved. Flow rate was corrected to the rate it would have been at 20 °C and then used to calculate K_s in the following equation:

$$[1] \quad K_s = \frac{Ql}{A_{\text{sample}} \Delta P}$$

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

Wood anatomic analyses

After K_s was measured, we made 30–40 μm thick transverse sections of each sample with a sliding microtome. We stained the sections with safranin and mounted them on slides with glycerine. We viewed the slides using a compound microscope (Eclipse E400, Nikon Inc., Melville, N.Y.) fitted with a camera (CoolSnap, Roper Scientific Photometric, Tucson, Ariz.) and made measurements using image software (version 4.0.2, Scion Corp., Frederick, Md.).

For each sample, we measured growth ring width, earlywood width, and latewood width on all growth rings that were fully formed within the approximately 1 cm^2 conductivity sample. We estimated the transition from earlywood to latewood visually as a distinct difference in cell wall thickness, which approximated Mork's definition of a latewood tracheid as one in which the width of the common cell wall

multiplied by two is equal to or greater than the width of an individual lumen (Denne 1988). Average latewood proportion in each sample was estimated as the average of the latewood proportion of each growth ring in the sample.

To obtain an estimate of tracheid diameter, we used two random rows of earlywood tracheids per growth ring excluding the first or last several tracheids within the earlywood zone. Tracheids were measured in the radial direction. Measurement included the lumen and the single cell wall on either side of the lumen.

To measure tracheid length, we made macerations of wood from each of the K_s samples taking care to sample only from the earlywood. Macerations were made by taking matchstick-sized pieces of the earlywood and putting them into a test tube with a solution of sodium chlorite and acetic acid. The test tubes were then placed in a waterbath at 80 °C for 2–3 h or until the wood looked bleached and frayed. The wood was then rinsed with water and a small portion of the now separated tracheids were mounted in glycerine on glass slides. We measured tracheid length using a stereoscopic zoom microscope (SMZ-2T, Nikon Inc., Melville, N.Y.) fitted with a camera (Pulnix, Motion Analysis Inc., Eugene, Ore.). Using image software (version 1.60, National Institutes of Health, Bethesda, Md.), we measured 50 tracheids per slide and three slides for each K_s sample for a total of 150 tracheids per sample. Additionally, we made sure that we only measured tracheids that had two tapered ends to avoid including tracheids that had been cut or broken.

Moisture content, wood density, and relative water content

After obtaining a fresh mass (M_f) of the moisture content disks in the field, we determined each disk's volume using the water submersion method. We then placed the disks in a drying oven at 50 °C for approximately 1 week and measured dry mass (M_d). We used the sample fresh and dry masses to calculate moisture content (MC) as follows:

$$[2] \quad \text{MC} = \frac{M_f - M_d}{M_d} \times 100$$

Then we used dry mass and fresh volume (V_f) to calculate wood density (D_w) as follows:

$$[3] \quad D_w = \frac{M_d}{V_f}$$

We then calculated relative water content of each disk as follows:

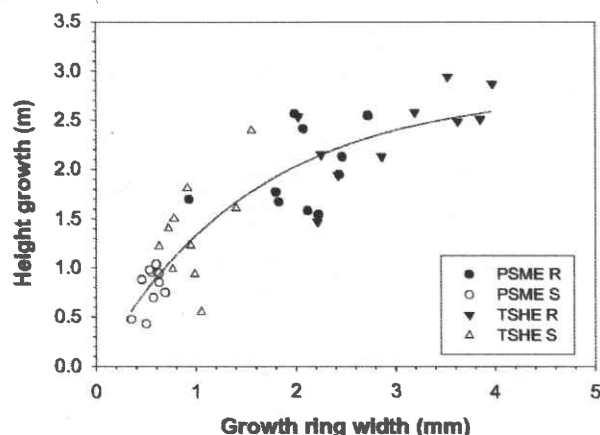
$$[4] \quad \text{RWC} = \frac{M_f - M_d}{(V_f - V_s) \rho}$$

where V_s is the volume of solid material calculated as dry mass divided by the density of cell wall material ($1.53 \text{ g} \cdot \text{cm}^{-3}$) (Siau 1984) and ρ is the density of water at 4 °C ($\text{g} \cdot \text{cm}^{-3}$).

Statistical analyses

Data were analyzed using a two-factor ANOVA with treatment (suppressed and released) and species (Douglas-fir and western hemlock) as the independent factors and the variables listed in Table 1 as dependent variables. Because there was only one site available to us with this 6-year-old treat-

Fig. 1. Relationship between height growth and growth ring width ($r^2 = 0.76$, $p < 0.0001$). PSME, Douglas-fir; TSHE, western hemlock; R, released; and S, suppressed.



ment, rather than site averages, as the experimental unit. Rather than study randomly selected trees, we used trees that fit within a specific height range. This selection decreased variation in the results that would have been caused by studying trees with highly variable size.

Means, 95% confidence intervals, and p values were calculated for all variables in Table 1 using SAS version 9.1 (SAS Institute Inc., Cary, N.C.). If needed, log transformations on the data were made to meet assumptions of normality and constant variance. If log transformations were made, the means and confidence intervals 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 with a p value of ≤ 0.05 were deemed significant. Relationships for regression were chosen based on the research questions in this study and significance in the relationships ($r^2 > 0.30$). Values of r^2 were obtained using SigmaPlot (version 9.01, SYSTAT Software Inc., Richmond, Calif.).

Results

The ages of suppressed and released trees did not differ significantly within either species, but western hemlock trees were younger on average than Douglas-fir trees (Table 1). Average width of the outer growth rings increased significantly in both Douglas-fir and western hemlock after release from suppression (Table 1) and was 3.7 and 3.0 times larger in released versus suppressed Douglas-fir and western hemlock, respectively (Table 1). Similarly, there was a positive relationship between growth ring width and height growth (Fig. 1). Species-specific regressions were very similar; therefore, the data were pooled, and only one line was fit. The relationship was also nonlinear in that, as growth ring width increased, height growth became independent of ring width.

Earlywood width was approximately four times greater in released than suppressed trees of both species. The relative increase in latewood width between suppressed and released trees was much greater in Douglas-fir than in western hemlock (Table 1). Therefore, the proportion of latewood in the

Fig. 2. Relationship between growth ring width and (A) earlywood width ($r^2 = 0.97$, $p < 0.0001$) or (B) latewood width for Douglas-fir ($r^2 = 0.90$, $p < 0.0001$) and western hemlock ($r^2 = 0.26$, $p = 0.02$). See Fig. 1 for abbreviations.

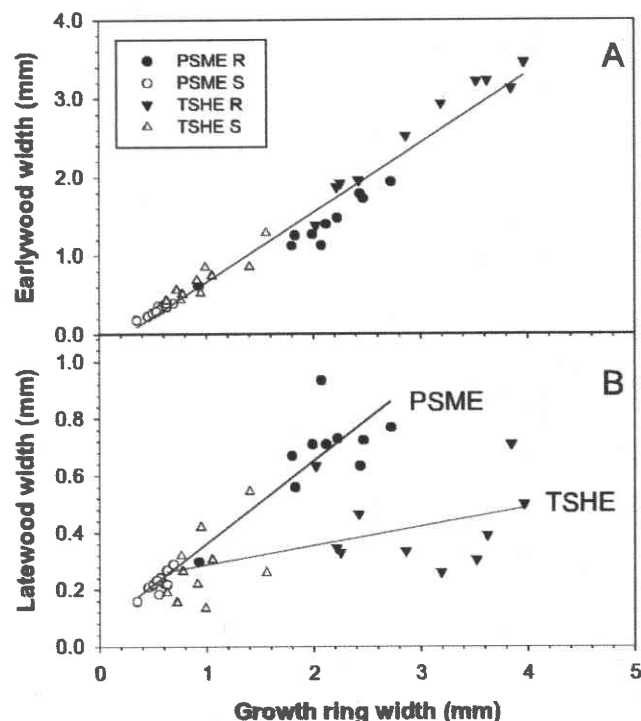
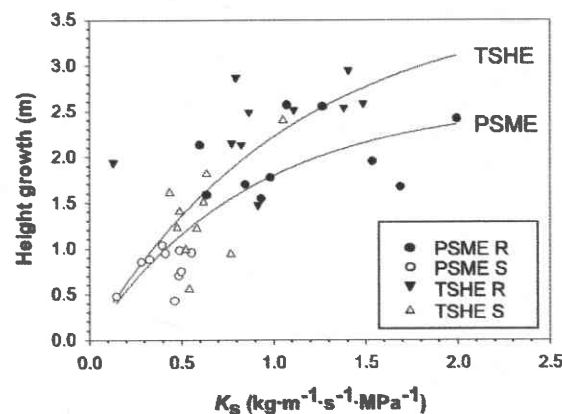


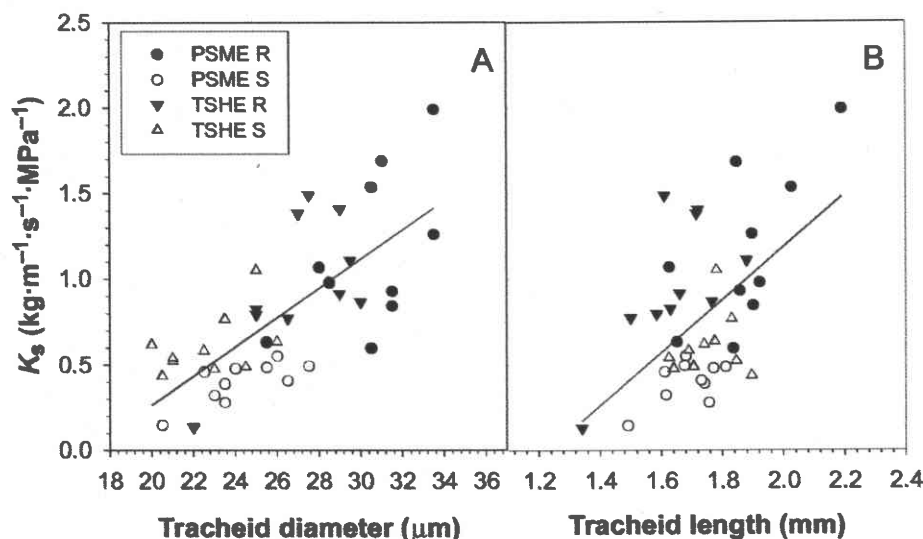
Fig. 3. Relationship between height growth and specific conductivity (K_s) for Douglas-fir ($r^2 = 0.64$, $p < 0.0001$) and western hemlock ($r^2 = 0.37$, $p = 0.0047$). See Fig. 1 for abbreviations.



growth ring decreased by 21% in released Douglas-fir compared with suppressed trees and by 47% in released western hemlock compared with suppressed trees.

The overall relationship between earlywood width and growth ring width was very strong for both Douglas-fir and western hemlock combined (Fig. 2A). In contrast, the relationship between latewood width and growth ring width appeared to be species specific with Douglas-fir showing increasingly

Fig. 4. Relationship between specific conductivity (K_s) and (A) tracheid diameter ($r^2 = 0.54$, $p < 0.0001$) or (B) tracheid length ($r^2 = 0.30$, $p = 0.0003$). See Fig. 1 for abbreviations.



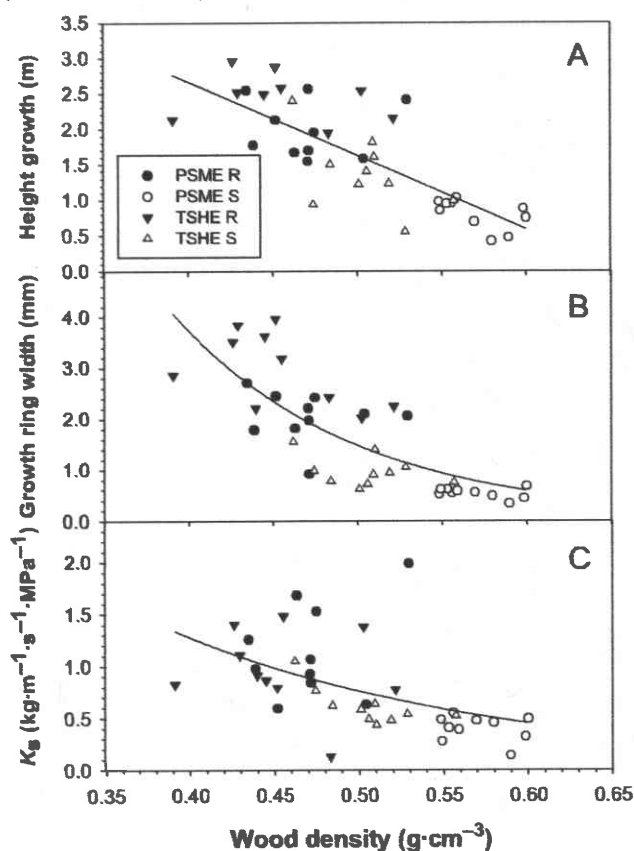
greater latewood width than western hemlock as total growth ring width increased (Fig. 2B). Although the data in Fig. 2B imply that species-specific trends should also be evident in Fig. 2A, the relationship for the pooled data was strong because latewood width was consistently small in western hemlock.

In both Douglas-fir and western hemlock, released trees had significantly higher K_s than did suppressed trees, although the relative differences were larger in Douglas-fir (Table 1). There was also a significant positive relationship between height growth and K_s for both Douglas-fir and western hemlock with Douglas-fir showing a smaller increase in height growth for a given increase in K_s than western hemlock (Fig. 3). Again, as with growth ring width, the relationship between height growth and K_s for both Douglas-fir and western hemlock was nonlinear in that as K_s increased, differences in height growth became independent of K_s .

In Douglas-fir, both tracheid diameter and tracheid length were significantly greater in released trees than in suppressed trees (Table 1). For western hemlock, however, only tracheid diameter increased significantly when trees were released from suppression. Although both tracheid diameter and length were positively correlated with K_s in both species (Figs. 4A and 4B), K_s was more closely associated with tracheid diameter than tracheid length. Because separate species-specific regression lines had overlapping 95% confidence intervals, the data were pooled in both cases, and only one line was fit.

In both Douglas-fir and western hemlock, wood density was significantly lower after release from suppression (Table 1). There were significant negative relationships between wood density and all of the following factors: height growth, growth ring width, and K_s for both species (Figs. 5A–5C). Again, species-specific regression lines had overlapping 95% confidence intervals, so we pooled the data and only fit one line. The relationships between wood density and both growth ring width and K_s were nonlinear in that, as wood density increased, the rate of decline in growth

Fig. 5. Relationship between wood density and (A) height growth ($r^2 = 0.59$, $p < 0.0001$), (B) growth ring width ($r^2 = 0.61$, $p < 0.0001$) or (C) specific conductivity (K_s) ($r^2 = 0.35$, $p = 0.0005$). See Fig. 1 for abbreviations.



ring width and K_s diminished. For both Douglas-fir and western hemlock, moisture content and relative water content increased significantly after trees released from suppression (Table 1).

Discussion

Anatomic changes that occur with release

Both young Douglas-fir and young western hemlock appear to release from suppression by making more wood, as shown by growth ring width, and by making wood with much higher K_s by increasing earlywood tracheid length and diameter and decreasing latewood proportion, compared with trees that remained suppressed. Similar responses have been observed in other studies. For example, Reid et al. (2003) found that K_s of sapwood of dominant lodgepole pines was 2.7 times greater than that of suppressed lodgepole pines. Sellin (1993) also found that the relative conductivity of open-grown Norway spruce was 1.4–3.1 times greater than shade-grown trees. However, other results contradict those found in this study. Jaakola et al. (2005b), Dutilleul et al. (1998), and Erickson and Harrison (1974) found that increased growth due to thinning was associated with decreased tracheid length, and Markstrom et al. (1983) found no effect of thinning on tracheid length.

K_s was positively related to both tracheid diameter and length. The relationship between K_s and tracheid diameter is expected, given the Hagen–Poiseuille equation, which states that flow through conduits is related to the radius of the conduits raised to the fourth power (Zimmermann 1983). However, the strength of the relationship between K_s and tracheid diameter is variable. Pothier et al. (1989) found that K_s was positively correlated with tracheid diameter in jack pine (*Pinus banksiana* Lamb.) trees between the ages of 15 and 35 years but not in older trees. They also found that K_s was never more than 60% of that predicted by the Hagen–Poiseuille equation. This discrepancy was reconciled by Lancashire and Ennos (2002), who found that resistance to flow through bordered pits made up a significant proportion of the total resistance of flow through tracheids and that the proportion of the total resistance that was caused by pits increased with tracheid diameter. Therefore, wider tracheids also need to be longer with more bordered pits connecting their overlapping portions to minimize resistance in the pathway. Models by Hacke et al. (2004) also show that short tracheids have low conductivity because they are limited by the conductivity of the bordered pits, and as tracheids increase in length, they become limited by their lumen diameter.

A relationship between K_s and tracheid length was also found in this study. However, whereas tracheid diameters were evenly scattered throughout the range of data (Fig. 4A), tracheid lengths for most of the trees seemed to be clustered between 1.6 and 2.0 mm (Fig. 4B) with the few trees with significantly longer or shorter tracheids making the linear relationship discernible. These patterns make sense given the tradeoffs of conductivity against safety where tracheid length is concerned. Although increases in tracheid length reduce the number of bordered pits that need to be crossed in the overall path from the ground to the leaves, longer tracheids also mean that a proportionally larger region of the conducting pathway will be lost if cavitation of these longer tracheids

occurs (Comstock and Sperry 2000). Therefore, whereas tracheid length is probably not an important variable for most trees that tend to have an average tracheid length, it can have major impacts on specific conductivity and redundancy in the conducting pathway when length is shifted above or below an average value.

Although height growth was correlated with both growth ring width and K_s , the relationship between height growth and growth ring width was stronger than the one between height growth and K_s , much more so for western hemlock than for Douglas-fir. Thus, larger increases in the number of tracheids as opposed to the efficiency of individual tracheids may be an important safety mechanism for trees that release from suppression. Larger tracheids that would be more efficient at water transport are also more vulnerable to embolism (Sperry and Tyree 1990). Therefore, making a greater number of tracheids with lower water conducting efficiency may prove less risky than making fewer, more efficient tracheids because it would result in decreased vulnerability to embolism and a greater redundancy in the system in the event that some tracheids are lost to embolism (Cruiziat et al. 2002).

The relationships of height growth with either growth ring width or K_s also appeared to be asymptotic. This pattern implies that water transport capacity of the main stem limits height growth in trees with narrow growth rings and low K_s ; however, as growth ring width and K_s increase, other factors begin to limit height growth. This limitation could result from an insufficient increase in the water transport capacity of the root system in released trees or limitations on increasing the photosynthetic capacity of the leaf tissue, thereby limiting whole-tree carbon fixation (Renninger et al. 2006).

Effects of release on wood density

The other main question addressed in this study was how wood density is affected by changes in growth rate that occur after release from suppression in young trees. Wood density was negatively related to height growth, growth ring width, and K_s . Therefore, increases in either growth ring width or K_s led to decreases in wood density. This is in agreement with Johnson et al. (2005) who found that wood density was positively correlated with the number of growth rings per centimetre in Douglas-fir trees affected by a foliar pathogen, but other studies in Douglas-fir are less conclusive (McKimmy 1959; Cown 1976; Abdel-Gadir et al. 1993).

The relationship between wood density and growth ring width will depend on how earlywood density, latewood density, and latewood proportion change as growth ring width changes. Several species of southern pine trees under moisture stress have been found to initiate latewood formation sooner than trees that are well watered (Zahner et al. 1964; Cregg et al. 1988). Therefore, because of increased competition by overstory trees, the suppressed trees in this study could be under more moisture stress than the released trees and would initiate latewood formation sooner and, thus, have a larger proportion of latewood per growth ring. This would give suppressed trees higher wood densities and greater water storage capacities given that latewood has a higher water storage capacity than earlywood (Domec and Gartner 2002). If earlywood width is driven by the leaf area the tree will develop, then the larger leaf areas of the released trees could

be the driver for wider earlywood and lower latewood proportion. Because earlywood has 11 times the K_v of latewood in Douglas-fir, growth rings with a higher proportion of earlywood will be more conductive and have lower wood density (Domec and Gartner 2002).

Douglas-fir exhibited a strong linear relationship between both earlywood and latewood width with growth ring width. However, for western hemlock, growth ring width was more strongly related to earlywood width than latewood width. This means that increases in growth ring width in western hemlock will correspond to increases in earlywood width but not necessarily with increases in latewood width. DeBell et al. (1994) found that wood density was negatively correlated with ring width in western hemlock and that latewood percentage dropped significantly with increasing ring width. However, Watson et al. (2003) found that wood density of 38-year-old western hemlock trees planted at different spacings (and with presumably different growth rates) was not significantly different. Some of this discrepancy can be reconciled by considering the age of the trees in that the negative relationship between growth rate and wood density is strongest in young western hemlock trees, decreases with time, and becomes insignificant in trees after age 30 years (DeBell et al. 2004). Therefore, relationships in this study between growth ring width and earlywood and latewood width in relatively young western hemlock trees may change as the trees age.

One aspect that could be a confounding factor in this research is the difference in ages between the Douglas-fir and western hemlock trees studied. The age of the western hemlock samples could have been underestimated because of missing rings in the suppressed region of the wood. However, it is more likely that the age difference was caused by our design of choosing trees on the basis of height: younger western hemlock trees would be of a similar height to older Douglas-fir trees given that western hemlock grew faster than Douglas-fir in both suppressed and released conditions (Renninger et al. 2006). The differences in age could be a problem when comparing wood characteristics between the two species because the samples would be coming from different positions within the juvenile zone. However, Fabris (2000) found that changes in wood properties in the juvenile zone of western hemlock were more gradual than for Douglas-fir. Therefore, age of the wood in western hemlock should not be as much of an issue as it could be in other species.

Although wood density has been shown to decrease after release from suppression, values of wood density for released Douglas-fir and western hemlock in the present study are only slightly lower than those reported for open-grown trees (Simpson and TeaWolde 1999). Therefore, if maintenance of some threshold wood density is an important determinant for the way the wood will be utilized, then release from suppression should not have deleterious effects on wood quality for these species. Furthermore, trees that have experienced suppression during the beginning of their lives may be better from a wood utilization standpoint because they will have a smaller core of juvenile wood in their lower log, increased wood density in their core wood, and fewer knots because of self-pruning of the lower branches that has occurred when trees were suppressed. However, if more subtle characteristics should prove to be important, such as the ho-

mogeneity of growth ring width, wood density or moisture content, then released trees may have wood with very different value than trees that were never suppressed.

Acknowledgments

This research was funded by a special grant from the USDA to Oregon State University for wood utilization research. We thank Hannah Dieterich for assistance in the field and J.C. Domec and John Tappeiner for advice and discussion. We thank the Bureau of Land Management for permission to study on their lands and three reviewers for comments on an earlier draft.

References

- Abdel-Gadir, A.Y., Krahmer, R.L., and McKimmy, M.D. 1993. Intra-ring variations in mature Douglas-fir trees from provenance plantations. *Wood Fiber Sci.* 25: 170–181.
- Comstock, J.P., and Sperry, J.S. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. *New Phytol.* 148: 195–218.
- Cown, D.J. 1976. Densitometric studies on the wood of young coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Ph.D. dissertation, University of British Columbia, Vancouver, B.C.
- Clegg, B.M., Dougherty, P.M., and Hennessey, T.C. 1988. Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. *Can. J. For. Res.* 18: 851–858.
- Cruziat, P., Cochard, H., and Ameglio, T. 2002. Hydraulic architecture of trees: main concepts and results. *Ann. For. Sci.* 59: 723–752.
- DeBell, D.S., Singleton, R., Gartner, B.L., and Marshall, D.D. 2004. Wood density of young-growth western hemlock: relation to ring age, radial growth, stand density and site quality. *Can. J. For. Res.* 34: 2433–2442.
- DeBell, J.D., Tappeiner, J.C., and Krahmer, R.L. 1994. Wood density of western hemlock: effect of ring width. *Can. J. For. Res.* 24: 638–641.
- Denne, M.P. 1988. Definition of latewood according to Mork (1928). *IAWA J.* 10 (1): 59–62.
- Domec, J.C., and Gartner, B.L. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees*, 15: 204–214.
- Domec, J.C., and Gartner, B.L. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? *J. Exp. Bot.* 53: 2369–2379.
- Dutilleul, P., Herman, M., and Avella-Shaw, T. 1998. Growth rate effects on correlations among ring width, wood density, and mean tracheid length in Norway spruce (*Picea abies*). *Can. J. For. Res.* 28: 56–68.
- Erickson, H.D., and Harrison, A.T. 1974. Douglas-fir wood quality studies part I: Effects of age and stimulated growth on wood density and anatomy. *Wood Sci. Technol.* 8: 207–226.
- Ewers, F.W. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *IAWA J.* 6(4): 309–317.
- Fabris, S. 2000. Influence of cambial ageing, initial spacing, stem taper and growth rate on wood quality of three coastal conifers. Ph.D. dissertation. University of British Columbia, Vancouver, B.C.

- Green, D.W., Lowell, E.C., and Hernandez, R. 2005. Structural lumber from dense stands of small-diameter Douglas-fir trees. *For. Prod. J.* **55** (7/8): 42–50.
- Hacke, U.G., Sperry, J.S., and Pittermann, J. 2004. Analysis of circular bordered pit function II. Gymnosperm tracheids with torus-margo pit membranes. *Am. J. Bot.* **91**: 386–400.
- Jaakkola, T., Mäkinen, H., and Saranpää, P. 2005a. Wood density in Norway spruce: changes with thinning intensity and tree age. *Can. J. For. Res.* **35**(7): 1767–1778.
- Jaakkola, T., Mäkinen, H., Sarén, M.P., and Saranpää, P. 2005b. Does thinning intensity affect the tracheid dimensions of Norway spruce? *Can. J. For. Res.* **35**(11): 2685–2697.
- Johnson, G.R., Grotta, A.T., Gartner, B.L., and Downes, G. 2005. Impact of the foliar pathogen Swiss needle cast on wood quality of Douglas-fir. *Can. J. For. Res.* **35**(2): 331–339.
- Kutscha, N.P., and Sachs, I.B. 1962. Color tests for differentiating heartwood and sapwood in certain softwood tree species. USDA For. Serv. For. Prod. Lab. Rep. No. 2246. pp. 1–13.
- Lancashire, J.R., and Ennos, A.R. 2002. Modeling the hydrodynamic resistance of bordered pits. *J. Exp. Bot.* **53**: 1485–1493.
- Larson, P.R. 1969. Wood formation and the concept of wood quality. *Yale Univ. Sch. For. Bull.* **74**: 24–53.
- Levan-Green, S.L., and Livingston, J. 2001. Exploring the uses for small-diameter trees. *For. Prod. J.* **51**: 10–21.
- Margolis, H.A., Gagnon, R.R., Pothier, D., and Pineau, M. 1988. The adjustment of growth, sapwood area, heartwood area, and sapwood saturated permeability of balsam fir after different intensities of pruning. *Can. J. For. Res.* **18**: 723–727.
- Markstrom, D.C., Troxell, H.E., and Boldt, C.E. 1983. Wood properties of immature ponderosa pine after thinning. *For. Prod. J.* **33**: 33–36.
- McKimmy, M.D. 1959. Factors related to variation of specific gravity in young-growth Douglas fir. Forest Products Research Center, Corvallis, Ore. Bull. No. 8.
- Miller, M., and Emmingham, B. 2001. Can selection thinning convert even-age Douglas-fir stands to uneven-age structures? *West. J. Appl. For.* **16**: 35–43.
- Minore, D. 1979. Comparative autecological characteristics of north-western tree species—a literature review. USDA For. Serv. Gen. Tech. Rep. PNW-87.
- O'Hara, K.L. 2001. The silviculture of transformation—a commentary. *For. Ecol. Manage.* **15**: 81–86.
- Pothier, D., Margolis, H.A., Poliquin, J., and Waring, R.H. 1989. Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can. J. For. Res.* **19**: 1564–1570.
- Reid, D.E.B., Silins, U., and Lieffers, V.J. 2003. Stem sapwood permeability in relation to crown dominance and site quality in self-thinning fire-origin lodgepole pine stands. *Tree Physiol.* **23**: 833–840.
- Renninger, H.J., Meinzer, F.C., and Gartner, B.L. 2006. Hydraulic architecture and photosynthetic capacity as constraints on release from suppression in Douglas-fir and western hemlock. *Tree Physiol.* In press.
- Sellin, A. 1993. Resistance to water flow in xylem of *Picea abies* (L.) Karst. trees grown under contrasting light conditions. *Trees*, **7**: 220–226.
- Siau, J.F. 1984. Transport processes in wood. Springer, Berlin, Heidelberg, New York.
- Simpson, W., and TeaWolde, A. 1999. Physical properties and moisture relations of wood. In *Wood handbook: wood as an engineering material*. USDA For. Serv. Gen. Tech. Rep. FPL 113.
- Sperry, J.S., and Tyree, M.T. 1990. Water stress induced xylem embolism in three species of conifers. *Plant Cell Environ.* **13**: 427–436.
- Spicer, R., and Gartner, B.L. 1998. Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood. *Tree Physiol.* **19**: 777–784.
- Spies, T.A., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forest of the Cascade Mountains. *Can. J. For. Res.* **20**: 649–658.
- Watson, P., Garner, C., Robertson, R., Reath, S., Gee, W., and Hunt, K. 2003. The effects of initial tree spacing on the fibre properties of plantation-grown coastal western hemlock. *Can. J. For. Res.* **33**: 2460–2468.
- Zahner, R. and Oliver, W.W. 1962. The influence of thinning and pruning on the date of summerwood initiation in red and jack pines. *For. Sci.* **8**: 51–63.
- Zahner, R., Lotan, J.E., and Baughman, W.D. 1964. Earlywood-latewood features of red pine grown under simulated drought and irrigation. *For. Sci.* **10**: 361–370.
- Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York.
- Zobel, B.J., and van Buijtenen, J.P. 1989. Wood variation: its causes and control. Springer-Verlag, New York.