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Influence of Bravo fungicide applications on wood density and moisture content of Swiss needle cast affected Douglas-fir trees

G.R. Johnson[a,*], Barbara L. Gartner[b], Doug Maguire[c], Alan Kanaskie[d]

[a]USDA Forest Service, 3200 SW Jefferson Way, Corvallis, OR 97331, USA
[b]Department of Wood Science and Engineering, Oregon State University, Corvallis, OR 97331, USA
[c]Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA
[d]Oregon Department of Forestry, 2600 State Street, Salem, OR 97310, USA

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Abstract

Wood density, moisture content, tracheid width and cell wall size were examined in trees from plots that were sprayed for 5 years with chlorothalonil (Bravo®) fungicide to reduce the impact of Swiss needle cast (SNC) and from trees in adjacent unsprayed plots. The unsprayed (more heavily diseased) trees had significantly narrower sapwood, narrower growth rings, lower sapwood moisture content, and narrower tracheid cell wall thickness than did the sprayed (less heavily diseased) trees. Moreover, unsprayed trees had altered earlywood density—earlywood width relationships, higher latewood proportion, and higher overall wood density than the sprayed trees. We hypothesize: (1) that the decreased moisture content of diseased trees results from their poor carbon economy resulting in insufficient energy (photosynthate) to reverse sapwood embolisms, and (2) SNC decreases wood density relative to growth rate.

Keywords: Wood density; Growth rate; Swiss needle cast; Xylem embolism; Chlorothalonil

1. Introduction

Since the late 1980s, Swiss needle cast (SNC), caused by the native pathogen *Phaeocryptopus gaeumannii* (Rohde) Petrak, has become increasingly severe in plantations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in coastal Oregon and Washington, USA. More recently, this foliar disease has intensified in older, naturally established stands as well. Whereas effects on growth (Hansen et al., 2000; Maguire et al., 2002) and physiology (Manter et al., 2000) have been reported, there is very little information available about its effect on wood properties. Anecdotal observations suggest that SNC increases the proportion of latewood relative to earlywood; this shift in early/latewood proportion would be a logical outcome given that previous experimental work has demonstrated that the earlywood production is mostly dependent on old foliage and the latewood mostly on the new foliage (Onaka, 1950). Because SNC causes premature loss of the older foliage, one would expect a larger reduction in the earlywood than latewood increment. Studies in balsam fir and eastern larch have shown that defoliation can affect other wood properties as well (Filion and Cournoyer, 1995; Krause and Morin, 1995). Information on the effects of SNC on

* Corresponding author. Tel.: +1-541-750-7290; fax: +1-541-750-7329.
E-mail address: randyjohnson@fs.fed.us (G.R. Johnson).

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wood properties is critically important because Douglas-fir forms the base of an industry in the Pacific Northwest focused primarily on structural lumber.

In severely damaged stands, symptoms of SNC infection include yellowing and premature loss of foliage. Average annual volume growth loss associated with SNC in young Douglas-fir plantations on the north Oregon Coast was estimated to be 23% in 1996, with some plantations suffering more than 60% volume growth loss (Maguire et al., 2002). The disease impedes gas exchange in the needles by occluding stomates with fruiting bodies (pseudothecia) (Manter et al., 2000). New needles become infected in the spring and early summer shortly after they emerge from buds. The fungus grows in the intercellular spaces of the needle and eventually forms pseudothecia. The pseudothecia emerge through the stomates and release spores in the spring and early summer. The amount of fungus and number of pseudothecia increase with age of the needle until the needle is dropped (Hansen et al., 2000). In heavily infected stands, first-year needles become chlorotic the following spring and drop from the tree during the second growing season. The loss of foliage and the impaired function of needles remaining on the tree combine to reduce tree growth and vigor. Typically, healthy Douglas-fir retain needles for at least 5 years (Hood, 1982) but stands on the north Oregon Coast commonly retain needles for 3 years or less (Maguire et al., 2002). In severely damaged trees, only the current year's foliage is retained by the end of the growing season.

The objectives of this paper were to: (1) test the hypothesis that reducing infection by *P. gaeumannii* with aerial application of fungicide caused a change in wood properties relative to the untreated trees; and (2) quantify the effect of SNC on several growth parameters and wood quality attributes. We then interpret these results in terms of wood value and utilization.

2. Materials and methods

2.1. Study site

The Oregon Department of Forestry established a trial near Beaver, Oregon (45°18′N, 123°49′W) to examine the effectiveness of Bravo® fungicide (Chlorothalonil) in controlling SNC on Douglas-fir on a stand that was experiencing very severe SNC. The stand is located approximately 10 km from the coast, in the "fog belt" that typically has high levels of SNC. Site index (age 50) for the stand was estimated to be 36 m. Three paired 2.02 ha (5-acre) plots were established; one plot in each pair was aerial sprayed with Bravo fungicide for five consecutive years (1996–2000). The other plot in the pair was an unsprayed control and was located within 100 m of the sprayed plot. Each year, the fungicide was applied twice at a rate of 6.4 l/ha (5.5 pints/acre) by helicopter. The first application was applied in May when the new foliage had expanded to a length of 2–5 cm on 40% of the trees. The second application was applied when expansion rates had attained this level on 90% of the trees; approximately 10–14 days after the first spray.

2.2. X-ray densitometry field and lab procedures

In the fall of 2000, when the stand was 20 years old, growth plots were established within each of the six plots (three sprayed and three unsprayed). Trees were felled and breast-height disks were removed from approximately 10 trees in each plot for a total of 58 disks. Two pith-to-bark samples from each disk were examined ring-by-ring using X-ray densitometry. An air-dried radial strip was sawn from each disk and line-scanned with a direct-scanning X-ray densitometer, with one value every 100 μm along the 100 μm wide scan. Data were deconvoluted using standard methods following the Lambert–Beer law (e.g., Liu et al., 1988) to give a curve, each point of which is linearly proportional to density of the wood at a position along the sample. The previously determined curve for each strip was adjusted separately such that its mean density equaled the measured oven-dried density of the strip.

DendroScan software (Varem-Sanders and Campbell, 1996) was used to find the boundaries between growth rings (the steepest point between the maximum latewood density of 1 year and the minimum earlywood density of the next year) and between earlywood and latewood (the point within a growth ring that has the average density between minimum earlywood and maximum latewood densities). These boundaries were then verified by comparison of graphs to samples. These definitions of the boundaries between growth rings and between earlywood and latewood are fixed within the software, but they matched our visual

determinations (by color) well. Data then were summarized for each growth ring to give the following values: growth ring density (total, earlywood, latewood), growth ring width (total, earlywood, and latewood), and latewood proportion.

2.3. Cell dimension measurements

From the same sample of trees analyzed by X-ray densitometry, three trees were randomly selected from each plot (18 trees total) and examined to determine tracheid width (lumen diameter) and double cell wall thickness. Transverse sections were made with a sliding microtome, then stained with safranin, and mounted permanently for analysis. The sections included the second growth ring (1999 growing season) inward from the cambium. The 1999 growth ring was chosen because it had been impacted by the spraying and would not have been affected by the removal of the bark from the sample. For both the earlywood and latewood in the 1999 ring, 15 tracheids from three separate regions (45 tracheids from the earlywood and 45 from the latewood) were measured in the radial direction for tracheid width and double cell wall thickness for each of the 18 trees. Values for double cell wall thickness were divided by 2 and are reported as cell wall thickness. The first and last-formed tracheids were avoided for measurements because they are often anomalous.

2.4. Moisture content field and lab procedures

Moisture content of the sapwood and heartwood was examined on 30 May 2001 (120 trees total) and 10 September 2001 (116 trees total) from a separate sample of trees. Approximately 20 dominant trees in each of the six plots (three sprayed and three unsprayed controls) were cored with a 5 mm increment borer from bark to pith. Cores were collected from both treatments simultaneously in a block. Treatments were randomly assigned to each of the two persons coring the trees. Immediately after removal, each core was wrapped tightly in plastic wrap. Cores were carried to the cooler after 10 cores were taken, and then again after the second 10 cores were taken from each plot. A third person began separating and weighing cores once the first set was received. Cores were divided into sapwood and heartwood on the basis of color and weighed to the nearest 0.001 g. Core length was measured to the nearest mm in order to obtain green volume. Time of collection and time of weighing were noted for each core. Approximately half of the cores were weighed within an hour of collection on site, the remaining half were divided and weighed the same day or the following day (September cores only) in the lab.

Density and moisture content were determined by obtaining green (fresh) mass, ovendry mass and core length. By using a wood density conversion factor of 1.53 g/cm^3 for pure cell wall material (Kellogg and Wangaard, 1969; Siau, 1984), the volume of wood, water and gas in the wood were estimated as follows:

- Core volume (cm^3) = core length $\times \pi \times (0.25)$.
- Moisture content (percentage on an ovendry mass basis) = 100 × [(green mass − dry mass)/dry mass].
- Green density (g/cm^3) = green mass/green volume.
- Basic density (g/cm^3) = dry mass/green volume.
- Percentage water (by volume) = 100 × [(green mass − dry mass)/green volume].
- Percentage of wood (by volume) = 100 × [(dry mass/1.53)/green volume].
- Percentage of gas (by volume) = 100 − percentage of water − percentage of wood.

2.5. Companion study

A companion study examined the percentage of wood, water and gas in earlywood and latewood. Fifteen dominant trees were cored with 10 mm increment cores from a 23-year-old plantation in McDonald-Dunn Experimental Forest located outside of Corvallis, OR (44°29′N, 123°16′W). Cores were wrapped individually in plastic wrap immediately after removal from the tree and placed into a cooler. They were returned to the lab within 3 h and processed. The last growth ring was removed and the next two growth rings (growing seasons 1999 and 2000) were divided into earlywood and latewood with a razor blade. Demarcation of earlywood and latewood was based on color change. Green mass was measured and volume obtained by submersion in mercury following ASTM 2395-93, method D (ASTM, 1999). Ovendry mass was obtained after 48 h at 103 °C. From these measurements the wood proper-

ties of the earlywood and latewood were calculated (moisture content, basic density, and volumetric percentage of water, wood, and gas).

2.6. Statistical models

Examination of the growth increments indicated that the fungicide treatments had affected growth primarily in the last 3 years. Therefore, only the overall means of the last three rings were subjected to statistical analyses for the density and growth data obtained from X-ray densitometry. The regression analyses used the MIXED procedure of SAS (1999) assuming the following statistical model:

$$\text{Wood property}_{ijk} = \mu + \text{Block}_i + \text{Treatment}_j + \text{Block} \times \text{treatment}_{ij} + e_{ijk} \quad (1)$$

where $\text{Wood property}_{ijk}$ is the value of the wood property for the kth tree in the ith block of jth treatment, μ the overall mean, Block_i the random effect of the ith block, i.e., which pair of plots, Treatment_j the fixed effect of the jth treatment (unsprayed control or Bravo-sprayed), $\text{Block} \times \text{treatment}_{ij}$ the random effect interaction of the ith block and the jth treatment, and e_{ijk} the residual variation associated with the among tree variation within each block–treatment subplot.

The appropriate error term for the treatment effect was the block × treatment interaction with only 2 degrees of freedom. If the block effect was not significant, the block effect was pooled with the interaction to bring the denominator degrees of freedom for the F-test to 4.

Earlywood density and latewood density were also subjected to a covariate analysis where earlywood width and latewood width were used as covariates. Analysis of covariance facilitated assessment of the marginal effect of SNC on wood density for a given growth rate.

Moisture content can be affected by collection time and, if drying occurs after core extraction, lag time between collection and measurement. To examine these effects, the model for analyzing moisture content was modified to

$$\text{Moisture content}_{ijk} = (b_1 \times \text{Collection time}) + (b_2 \times \text{Measurement time lag}) + \text{Block}_i + \text{Treatment}_j + \text{Block} \times \text{treatment}_{ij} + e_{ijk} \quad (2)$$

where b's are the regression coefficients for collection time and measurement time (i.e. covariates), and the other independent variables are the same as in Eq. (1).

Means and standard errors were computed with the least-square means option of the MIXED procedure of SAS (1999).

3. Results

3.1. X-ray densitometry data

Radial growth of the trees sprayed with Bravo appeared to have recovered to a "normal" rate by 1998 (after 2 years of spraying) (Table 1). Growth during the last 3 years was significantly reduced in both the earlywood and latewood growth rings of the unsprayed trees (Table 2), with the greatest difference in the earlywood. This pattern resulted in a higher proportion of latewood in the unsprayed plots than the sprayed plots (Table 2, 52 vs. 41%, $P < 0.0001$), which in turn, increased the ring density in the unsprayed plots (0.589 vs. 0.524, $P = 0.1025$). The unadjusted means of earlywood and latewood density were not statistically different between the treatments.

Ring density and earlywood density in the outer three rings were correlated significantly ($P < 0.0001$) with ring width and earlywood width ($r = -0.67$ and -0.56, respectively). Latewood density did not have a significant correlation with latewood width for these three rings ($r = -0.08, P = 0.56$). Regression analyses demonstrated a statistically different ($P = 0.01$) relationship between earlywood width and earlywood density for the two treatments; different equations were needed to represent the relationship between earlywood width and earlywood density for each treatment group. The different relationship for each treatment group was true whether the relationship was modeled as a simple linear function or as a negative exponential function. The negative exponential function relationship was close to linear for the data if separate models were generated for each treatment group, therefore, the simple linear relationship for the controls and Bravo-sprayed trees is shown in Fig. 1. The range of earlywood widths differed for the two groups as well, and had very little overlap (Fig. 1).

Table 1
Average earlywood, latewood and total ring widths (cm) and latewood proportion by annual ring, as determined from growth plot disks, without (control) and with chloranthalonil spraying (Bravo) for approximately 30 sample trees in each treatment

Ring year	Ring width		Earlywood width		Latewood width		Latewood percentage	
	Control	Bravo	Control	Bravo	Control	Bravo	Control	Bravo
No spraying								
1991	0.59	0.53	0.26	0.21	0.33	0.32	58	61
1992	0.60	0.54	0.27	0.22	0.34	0.32	57	60
1993	0.66	0.65	0.34	0.32	0.32	0.33	49	53
1994	0.58	0.59	0.26	0.27	0.32	0.32	57	56
1995	0.47	0.47	0.23	0.21	0.24	0.26	53	57
Annual spraying begins								
1996	0.36	0.34	0.14	0.12	0.23	0.22	64	66
1997	0.40	0.47	0.16	0.18	0.24	0.29	61	62
1998	0.40	0.63	0.20	0.39	0.19	0.25	50	40
1999	0.33	0.60	0.15	0.35	0.17	0.25	54	43
2000	0.30	0.65	0.14	0.39	0.16	0.26	53	41

Table 2
Wood properties averaged for the outer three rings of trees that were unsprayed (control) and those sprayed with chloranthalonil (Bravo) fungicide (means, standard errors, and level of statistical difference (P-value))[a]

	Control		Bravo		P-value
	Mean	S.E.	Mean	S.E.	
Ring width (cm)	0.333	0.077	0.623	0.077	0.0081
EW width (cm)	0.164	0.053	0.373	0.053	0.0125
LW width (cm)	0.170	0.025	0.250	0.025	0.0876
LW percentage	52.0	1.9	41.4	1.9	<0.0001
Ring density (g/cm^3)	0.589	0.016	0.524	0.016	0.1025
EW density (g/cm^3)	0.376	0.016	0.362	0.016	0.5857[b]
LW density (g/cm^3)	0.777	0.009	0.775	0.009	0.8579
EW tracheid diameter (μm)	32.33	1.63	34.83	1.63	0.1949
LW tracheid diameter (μm)	11.05	0.58	7.28	0.58	0.0377
EW cell wall thickness (μm)	3.18	0.36	5.35	0.36	0.0004
LW cell wall thickness (μm)	5.70	0.22	5.62	0.22	0.8220

[a] Data is from 60 trees sampled in the growth plots, except for tracheid diameter and double cell wall thickness, which are from a subsample of 18, for the 1999 growth ring only. EW: earlywood; LW: latewood.
[b] Differences exist between treatments in the relationship between density and width.

3.2. Tracheid and double cell wall thickness

Earlywood cell wall thickness was larger in the sprayed trees than in the unsprayed trees (Table 2, 3.2 μm for the unsprayed vs. 5.4 μm for the Bravo-sprayed trees). Cell wall thickness of latewood did not differ between treatments. Earlywood tracheid diameters did not differ between treatments, but in the latewood, tracheid diameter was larger in the unsprayed trees (Table 2, 11.1 μm for the unsprayed trees and 7.3 μm for the sprayed trees).

3.3. Moisture content samples

Time of collection and time of measurement did not affect any variables in the May samples, but did affect the September moisture and gas contents ($P < 0.05$). The block effect was not statistically significant in either month for any trait ($P > 0.10$). Therefore, the block effect was dropped from the model and pooled with the block × treatment interaction.

As expected, there was a large difference between the sapwood and heartwood moisture contents

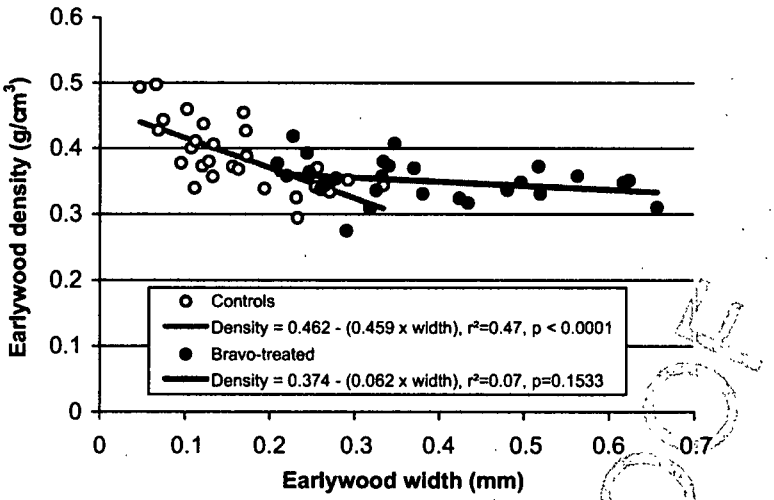

Fig. 1. Relationship between earlywood density and earlywood width in the outer three growth rings for Bravo-treated and control trees.

Table 3
Moisture content in sapwood and heartwood (means, standard deviations and coefficients of variation) for all sample trees

	Mean moisture content (%)	S.D. (%)	Coefficient of variation (%)
Sapwood (May, $n = 120$)	99	19.9	21
Heartwood (May)	36	2.3	6
Sapwood (September, $n = 116$)	94	21.6	23
Heartwood (September)	35	2.5	7

(Table 3). The amount of variation associated with the sapwood moisture content was considerably greater than that associated with the heartwood; coefficients of variation ((S.D./mean) × 100) were three times larger for the sapwood than the heartwood (Table 3).

In the heartwood, there were no significant relationships between the treatments for moisture content, wet or green density, sapwood width, sapwood area, or volumetric percentages of wood, water, or gas ($P > 0.05$, data not shown). However, there was a trend toward lower percentage of water in trees from the sprayed plots than the unsprayed plots, both in May (15.1 vs. 16.0%, respectively, $P = 0.0815$) and in September (14.6 vs. 15.4%, $P = 0.0670$). Further results are only reported for sapwood.

Sapwood width and area were greater in the sprayed plots (Table 4). On average, the sprayed trees had 35% more sapwood area than did the unsprayed trees.

At both dates, there was significantly lower moisture content in sapwood of trees in the unsprayed plots than trees in the sprayed plots. Sapwood moisture content in unsprayed plots and sprayed plots was 88 and 110%, respectively, in May, and 84 and 104% in September (Table 4). Similarly, the volumetric percentage of water was also lower in the unsprayed trees than the sprayed trees (42 and 40% vs. 50 and 47%, Table 4). This reduction in moisture came as a result of increased gas because there was a statistically significant increase in percentage of gas, but not in the percentage of wood (Table 4).

Because of the increased moisture content, the green density of the sapwood was higher in the Bravo-sprayed trees (Table 4). However, sapwood basic density was lower (though not statistically significant) in the sprayed trees than the unsprayed trees (Table 4). To understand whether the changes in the volumetric wood, water, and gas contents were simply a function of latewood percentage; the percentages of wood, water and gas were examined in 15 healthy trees in the McDonald-Dunn Forest. A simple t-test indicated that all three wood properties differed between the earlywood and latewood ($P = 0.001$, Table 5). The latewood had higher percentages of wood (35 vs. 18%) and gas (29 vs. 21%),

Table 4
Moisture content, wood density and volumetric percentage of wood, water and gas in the sapwood of trees that were not sprayed (control) vs. those that were sprayed with chloranthalonil (Bravo)[a]

Wood property	May sample ($n = 120$)					September sample ($n = 116$)				
	Control		Bravo		*P*-value	Control		Bravo		*P*-value
	Mean	S.E.	Mean	S.E.		Mean	S.E.	Mean	S.E.	
Moisture content (%)	**87.9**	**2.2**	**109.6**	**2.2**	**0.0020**	**84.6**	**4.8**	**104.6**	**4.8**	**0.0557**
Density (basic) (g/cm^3)	**0.480**	**0.007**	**0.458**	**0.007**	**0.0843**	**0.481**	**0.010**	**0.461**	**0.010**	**0.2459**
Density (green) (g/cm^3)	**0.897**	**0.008**	**0.954**	**0.008**	**0.0089**	**0.882**	**0.008**	**0.936**	**0.008**	**0.0197**
Sapwood width (cm)	**3.9**	**0.20**	**4.8**	**0.20**	**0.0552**	**4.1**	**0.13**	**5.1**	**0.13**	**0.0301**
Sapwood area (cm^2)	**175.5**	**18.6**	**238.7**	**18.6**	**0.1263**	**189.5**	**12.1**	**256.7**	**12.1**	**0.0174**
Percentage of wood	**31.3**	**0.44**	**29.9**	**0.44**	**0.0843**	**31.4**	**0.65**	**30.1**	**0.65**	**0.2459**
Percentage of water	**41.8**	**0.71**	**49.6**	**0.71**	**0.0014**	**40.4**	**1.46**	**47.5**	**1.46**	**0.0391**
Percentage of gas	**26.9**	**0.71**	**20.4**	**0.70**	**0.0029**	**28.2**	**0.97**	**22.4**	**0.97**	**0.0232**

[a] Reported are means, standard errors and *P*-values for two sample dates (May and September 2001). Comparisons in bold are statistically significant at $P = 0.05$.

Table 5
Moisture content, basic density (dry mass/fresh volume), and volumetric content of wood, water, and gas in earlywood vs. latewood of healthy Douglas-fir trees (means and standard deviations)[a]

Wood property	Earlywood		Latewood		*P*-value
	Mean	S.D.	Mean	S.D.	
Moisture content (%)	227.6	38.8	65.0	11.7	<0.0001
Basic density (g/cm^3)	0.272	0.033	0.550	0.043	<0.0001
Percentage of wood	17.8	2.2	35.9	2.8	<0.0001
Percentage of water	60.8	5.2	35.3	3.5	<0.0001
Percentage of gas	21.4	4.8	28.8	2.3	0.0003

[a] *t*-Test significance levels for comparing earlywood and latewood are reported.

and a lower percentage of water (35 vs. 61%) than the earlywood.

4. Discussion

The 5 years of spraying did not achieve complete control of the disease; significant amounts of *P. gaeumanni* were present in the needles of the sprayed trees during the fifth year of spraying (Stone et al., 2002). Nonetheless, needle retention increased for the last 3 years of spraying; the unsprayed trees carried about 1.9 years of foliage whereas the treated trees had 2.8 years of foliage (Mainwaring et al., 2002). The difference in foliage quantity was most pronounced in spring before the new foliage emerged. Therefore, during spring and early summer (when the new foliage was maturing), the trees in the sprayed plots were at a greater growth advantage because they had considerably more foliage producing photosynthate than the trees in the unsprayed plots. After the new foliage matured and became a net exporter of photosynthate, the advantage decreased. This pattern is consistent with our data on radial growth increments: the Bravo-sprayed plots had 68% more earlywood than the unsprayed plots, but only 44% more latewood. Increased availability of photosynthates is assumed to increase cell wall thickness (Larson, 1969; Savidge, 1996) and is a logical explanation for the increased cell wall thickness found in the earlywood of the treated trees.

Compared to the unsprayed trees, trees treated with fungicide showed increased radial growth rates, lower percentages of latewood, lower ring density and higher moisture contents. It appears that the sapwood of trees with severe SNC have a diminished capacity to trans-

port water relative to healthy trees. A decrease in sapwood water content is associated with a decrease in specific conductivity (Puritch, 1971; Edwards and Jarvis, 1982) and sap flow (Granier et al., 2000). Whereas our methods did not distinguish between water being transported in the tracheids and extracellular water (which is not being transported), the reduction in moisture content cannot be accounted for by extracellular water alone. Likewise, this difference was not solely the result of increased latewood, although de Kort (1993) demonstrated that latewood percentage impacts moisture content. de Kort (1993) found that a 1% increase in latewood percentage resulted in a 1.7% decrease in moisture content. Based on average sapwood width and average ring widths, the sapwood–heartwood boundary generally occurred at the 1992 growth ring for both the sprayed and control plots. The latewood percentage, weighted by ring width, for this time period (1992–2000) was 50.7% in the sprayed plots and 54.5% in the control. Using de Kort's (1993) relationship, the reduction in moisture content due to the increased latewood in the unsprayed plots would have been 6.5%. Similarly, the data from healthy trees on McDonald-Dunn Forest suggested a decrease of between 5 and 6% could be attributed to the higher latewood proportions. The 21% decrease in moisture content between the sprayed and unsprayed plots is, therefore, considerably more than the amount accounted for by the increased proportion of latewood.

Similarly, the increase in percent gas between the treatments cannot be explained by an increase in latewood. Healthy trees on McDonald-Dunn Forest exhibited a 7.4% absolute difference in the percentage of gas between the earlywood and latewood (28.8% gas vs. 21.4% gas, Table 5). The difference between the sprayed and control treatments in the Bravo study was very similar (6.5% in May and 5.8% in September, Table 4). The difference in latewood percentage for the sprayed and unsprayed trees in the Bravo plots was only 4%; not enough to account for the differences in the percent of gas.

We hypothesize that the decreased moisture content of diseased trees resulted from their poor carbon economy resulting in insufficient energy (photosynthate) to reverse sapwood embolisms. Air embolisms in the xylem can be refilled by trees, but the exact mechanism is unknown (Holbrook and Zwieniecki, 1999). Experiments with phloem-girdled stems suggest that photosynthate is required to refill an embolism in order to recover specific conductivity (Salleo et al., 1996; Zwieniecki and Holbrook, 1998) and moisture content (Taylor and Cooper, 2002; Wilson and Gartner, 2002). This reduction in moisture content could, therefore, be a function of the tree's poor vigor, preventing a phosynthate pool sufficient for reversing many of the gas embolisms that occur on a daily basis.

The reduction in sapwood area in the unsprayed trees was also expected. Sapwood area is related to the amount of foliage (Grier and Waring, 1974) and the unsprayed trees had less foliage as measured by the number of years that needles were retained.

The observed changes in wood properties have economic ramifications. For a given log size, log weights from the sprayed plots will be greater than those from the unsprayed plots. The sprayed trees have more sapwood, which is of higher green density than heartwood. Also, the moisture content of the sapwood is greater in the sprayed trees. The average green density of the entire pith-to-bark core for the May sample averaged 0.765 in the sprayed plots and 0.712 in the unsprayed plots. Based upon the breast-height disk, a load of logs from the sprayed plots would weigh approximately 7.4% more than an equal load (same volume) of unsprayed logs. However, there would be no difference between the dry masses of the loads because the basic densities were identical (0.445 in the unsprayed plots vs. 0.447 in the sprayed plots).

The reduced amount of sapwood in the unsprayed trees could also have negative consequences if one is selling the timber for poles or pilings. A minimum sapwood width (19 mm) is required to insure adequate preservative penetration (AWPA, 1999). Sapwood width averaged 9 mm less in the untreated than the treated trees. Even if a tree has sufficient sapwood, CCA (copper chromium arsenate) retention could be poor given the larger proportion of latewood in unsprayed trees and the fact that earlywood retains more CCA than latewood (Guo et al., 2002).

5. Conclusions

It is impossible to construct a study in coastal Oregon that examines infected and uninfected trees

without the use of fungicide because suitable healthy controls cannot be found. The healthy trees in this study are not simply trees with less SNC, instead, they have had repeated applications of Bravo fungicide. Therefore, one cannot state unequivocally that the observed changes in wood properties are the result of SNC alone; but rather that fungicide had an effect. However, if we assume that the fungicide simply reduced the amount of fungus, then several conclusions regarding SNC can be drawn. First, severe SNC reduced growth rate in a manner similar to that found by Maguire et al. (2002) and Mainwaring et al. (2002). Second, the growth depression was more severe in earlywood than in latewood, resulting in higher latewood proportion and wood density. In addition, the decline in tree vigor also adversely impacted the hydraulic properties of the stem by reducing the amount of sapwood and the moisture within the sapwood. Tracheid wall thickness was also reduced in the earlywood of severely infected trees.

Future research will look more closely at possible changes in the strength properties of wood coming from severely infected stands. The increased wood density resulting from increased proportions of latewood suggests potentially stronger wood. However, the weakest portion of wood is the earlywood and the reduced cell wall thickness found in this study suggests that the "weakest link" has been weakened.

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References

ASTM (American Society for Testing and Materials), 1999. Standard test methods for specific gravity of wood and wood-base materials, D-2395-93. Annual Book of ASTM Standards 4.10. Wood, West Conshohocken, PA.

AWP (American Wood-Preservers' Association), 1999. Standard C3-99. Piles—Preservative Treatment by Pressure Process. AWPA Book of Standards, Granbury, TX, pp. 51–64.

de Kort, I., 1993. Relationships between sapwood amount, latewood percentage, moisture content and crown vitality of Douglas-fir, *Pseudotsuga menziesii*. IAWA J. 14, 413–427.

Edwards, W.R.N., Jarvis, P.G., 1982. Relations between water content, potential and permeability in stems of conifers. Plant Cell Environ. 5, 271–277.

Filion, L., Cournoyer, L., 1995. Variation in wood structure of eastern larch defoliated by the larch sawfly in subarctic Quebec, Canada. Can. J. For. Res. 25, 1263–1268.

Granier, A., Biron, P., Lemoine, D., 2000. Water balance, transpiration and canopy conductance in two beech stands. Agric. For. Meteorol. 100, 291–308.

Grier, C.C., Waring, R.H., 1974. Conifer foliage mass related to sapwood area. For. Sci. 20, 205–206.

Guo, A., Cooper, P.A., Ung, Y.T., Ruddick, J.N.R., 2002. Comparison of fixation rates of earlywood, latewood, sapwood, and heartwood of CCA-treated Douglas-fir, southern pine, and eastern larch. For. Prod. J. 52, 77–80.

Hansen, E.M., Stone, J.K., Capitano, B.R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A., McWilliams, M.G., 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. Plant Dis. 84, 773–778.

Holbrook, N.M., Zwieniecki, M.A., 1999. Embolism repair and xylem tension: do we need a miracle. Plant Physiol. 120, 7–10.

Hood, I.A., 1982. *Phaeocryptopus gaeumannii* on *Pseudotsuga menziesii* in southern British Columbia. NZ J. For. Sci. 12, 415–424.

Kellogg, R.M., Wangaard, F.F., 1969. Variation in the cell-wall density of wood. Wood Fiber Sci. 1, 180–204.

Krause, C., Morin, H., 1995. Impact of spruce budworm defoliation on the number of latewood tracheids in balsam fir and black spruce. Can. J. For. Res. 25, 2029–2034.

Larson, P.R., 1969. Wood Formation and the Concept of Wood Quality. Bulletin No. 74. Yale University, School of Forestry.

Liu, C.J., Olson, J.R., Tian, Y., Shen, Q., 1988. Theoretical wood densitometry. I. Mass attenuation equations and wood density models. Wood Fiber Sci. 20, 22–34.

Maguire, D., Kanaskie, A., Voelker, B., Johnson, R., Johnson, G., 2002. Growth of young Douglas-fir plantations across a gradient in Swiss needle cast severity. West. J. Appl. For. 17, 86–95.

Mainwaring, D., Kanaskie, A., Maguire, D., 2002. Response of Douglas-fir to fungicidal suppression of *Phaeocryptopus gaeumannii*: volume growth, branch elongation, and foliage dynamics. In: Filip, G. (Ed.), Swiss Needle Cast Cooperative Annual Report 2002. Oregon State University, College of Forestry, Corvallis, OR, pp. 82–86.

Manter, D.K., Bond, B.J., Kavanagh, K.L., Rosso, P.H., Filip, G.M., 2000. Pseudothecia of Swiss needle cast fungus, *Phaeocryptopus gaeumannii*, physically block stomata of Douglas fir, reducing CO_2 assimilation. New Phytol. 148, 481–491.

Onaka, F., 1950. The effects of such treatments as defoliation, debudding, girdling, and screening of light in growth and especially on radial growth of evergreen conifers. Bull. Kyoto Univ. For. 18, 55–95.

Puritch, G.S., 1971. Water permeability of the wood of grand fir (*Abies grandis* (Dougl.) Lindl.) in relation to infestation by the

balsam wooly aphid, *Adelges piceae* (Ratz.). J. Exp. Bot. 22, 936–945.

Salleo, S., Lo Gullo, M., De Paoli, D., Zippo, M., 1996. Xylem recovery from cavitation-induced embolism in young plants of *Laurus nobilis*: a possible mechanism. New Phytol. 132, 47–56.

SAS, 1999. SAS/STAT® User's Guide, Version 8. SAS Institute, Inc., Cary, NC, 3884 pp.

Savidge, R.A., 1996. Xylogenesis, genetic and environmental regulation: a review. IAWA 17, 269–310.

Siau, J.F., 1984. Transport Processes in Wood. Springer, Berlin, p. 245.

Stone, J., Reeser, P., Kanaskie, A., 2002. Fungicidal control of Swiss needle cast in a 20-year-old forest stand. In: Filip, G. (Ed.), Swiss Needle Cast Cooperative Annual Report 2002. Oregon State University, College of Forestry, Corvallis, OR, pp. 53–57.

Taylor, A.M., Cooper, P., 2002. The effect of stem girdling on wood quality. Wood Fiber Sci. 34, 212–220.

Varem-Sanders, T.M.L., Campbell, I.D., 1996. DendroScan: a tree-ring width and density measurement system. Natural Resources Canada, Canadian Forest Service, Northern Forestry Center, Edmonton, Alberta.

Wilson, B.F., Gartner, B.L., 2002. Effect of stem girdling on conifers: apical control of branches, growth and air in wood. Tree Physiol. 22, 347–353.

Zwieniecki, M.A., Holbrook, N.M., 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). Plant Cell Environ. 21, 1173–1180.