Impact of the foliar pathogen Swiss needle cast on wood quality of Douglas-fir

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Abstract: Many stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) near coastal areas of Oregon and Washington are heavily infected with the foliar pathogen causing Swiss needle cast (SNC) disease, and yet there is very little research on the resulting wood quality. Modulus of elasticity (MOE), modulus of rupture (MOR), microfibril angle (MFA), wood density, latewood proportion, and sapwood moisture content were examined in 20- to 28-year-old trees from 15 stands that were infected with varying intensities of SNC. SNC severity was quantified by measuring needle retention, the number of needle cohorts retained at three crown levels. Correlations between disease severity and wood properties were examined at both the stand and within-stand levels. Trees from heavily infected stands (needle retention <2 years) had higher MOE, wood density, and latewood proportion and lower sapwood moisture content than trees from healthier stands. Breast-height age (BHage) was also correlated with these properties, but age alone did not explain all of the increases. MFA was not associated with SNC severity. Within stands, needle retention was not associated with MOE or MOR. The increase in latewood proportion in diseased stands appears to be the driving factor behind their increase in stiffness (MOE). Ring width decreased with decreased needle retention, and the examined wood properties generally showed stronger correlations with ring width than with needle retention.

Résumé : Plusieurs peuplements de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) situés près des régions côtières dans les États de l'Oregon et de Washington sont sévèrement infectés par un pathogène foliaire qui cause une maladie appelée rouge de Gauemann et l'impact de cette maladie sur la qualité du bois est peu connu. Le module d'élasticité (MOE), le module de rupture (MOR), l'angle des microfibrilles (AMF), la densité du bois, la proportion de bois final et la teneur en eau de l'aubier ont été étudiés chez des arbres âgés de 20 à 28 ans provenant de 15 peuplements infectés à divers degrés par la maladie. La sévérité de la maladie a été quantifiée en mesurant la rétention des aiguilles; le nombre de cohortes d'aiguilles présentes à trois niveaux dans la cime. Les corrélations entre la sévérité de la maladie et les propriétés du bois ont été étudiées tant à l'échelle des peuplements qu'entre les arbres d'un même peuplement. Les arbres dans les peuplements sévèrement infectés (rétention des aiguilles <2 ans) avaient un MOE, une densité du bois et une proportion de bois final plus élevés ainsi qu'une teneur en eau de l'aubier plus faible que les arbres dans les peuplements sains. L'âge à hauteur de poitrine était aussi corrélé avec ces propriétés mais l'âge seul n'expliquait pas toutes les augmentations. L'AMF n'était pas relié à la sévérité de la maladie. Dans un même peuplement, la rétention des aiguilles n'était pas reliée au MOE ou au MOR. L'augmentation de la proportion de bois final dans les peuplements malades serait le principal facteur dans l'augmentation de la rigidité (MOE). La largeur des cernes diminuait avec une diminution de la rétention des aiguilles et les propriétés du bois qui ont été étudiées ont généralement montré des corrélations plus étroites avec la largeur des cernes qu'avec la rétention des aiguilles.

[Traduit par la Rédaction]

Introduction

Swiss needle cast (SNC) is a foliar disease affecting Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the forests of the Pacific Northwest. The fungus causing the disease (*Phaeocryptopus gaeumannii* (Rohde) Petrak) has been known to foresters in the Pacific Northwest region of the United States since the early 20th century (Boyce 1940) but was not considered damaging until recently (Hansen et al. 2000). The disease impedes gas exchange in the needles by occluding stomates with fruiting bodies (pseudothecia) (Manter et al. 2000), resulting in chlorotic foliage and early casting of the needles (Hansen et al. 2000). As a result of a severe outbreak of SNC, growth has been negatively impacted in Douglas-fir plantations in coastal Oregon since the early 1990s (Maguire et al. 2002). Because the regional forest products sector relies heavily on wood from Douglas-fir plantations, any agent that affects the quality of this

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plantation-grown wood must be critically examined. Currently, information regarding the impact of SNC on Douglas-fir wood properties such as density, strength, and stiffness is limited.

Johnson et al. (2003) found that trees heavily infected with SNC had reduced sapwood area and lower sapwood moisture content and higher wood density than trees that had been sprayed with a fungicide to control the disease. The reduced amount of sapwood and lower moisture content suggested reduced hydraulic function as a result of SNC. The increase in wood density was linked to an increase in latewood proportion relative to sprayed trees. Assuming that the only effect of the fungicide was to reduce SNC severity, one might expect wood from diseased trees to be stiffer and stronger, because modulus of elasticity (MOE, a measure of stiffness) and modulus of rupture (MOR, a measure of strength) are both positively correlated with wood density (Green et al. 1999). Microfibril angle (MFA) of the cell wall also affects wood properties; wood with a lower mean MFA is stiffer (Cave 1969; Cave and Walker 1994) and stronger (Treacy et al. 2000). To date, no studies have investigated the effects of SNC on MFA, strength (MOR), or stiffness (MOE).

A fungicide study by Johnson et al. (2003) allowed a comparison between heavily infected trees and less-infected, fungicide-treated trees. Douglas-fir plantations in western Oregon exhibit a wide gradient of SNC severity (Kanaskie et al. 2002), and although the severity of symptoms within a stand fluctuates from year to year, the ranking of stands over time with respect to disease severity is relatively constant (Maguire et al. 2003). Because SNC causes premature needle loss, disease severity is typically quantified as the number of annual cohorts of needles retained on the tree; while healthy trees in this region typically have up to 5 years' worth of needles, diseased trees may have only 1–3 years' worth (Weiskittel 2003). In this study, we examined wood properties from stands across a gradient of SNC severity.

The objectives of this study were (1) to understand how SNC affects Douglas-fir MOE and MOR; (2) to identify the anatomical features (i.e. earlywood/latewood ratio, density, MFA) that underlie these relationships; and (3) to more closely examine the effect of SNC on wood properties by relating anatomical properties to needle retention.

Materials and methods

Sample collection and analysis

Fifteen stands were selected from an existing set of 70 Swiss needle cast monitoring stands (Maguire et al. 2002). The stands were all located along the western slope of the Oregon Coast range between Astoria to the north and Toledo to the south (Table 1). Stands were selected so that they fell within a relatively narrow band of site indices (38–43 m at age 50 years), and stand ages (20–28 years for breast-height age (BHage)), but with a wide range of needle retention values (1.53–3.03 years of needles). Needle retention values were defined as the number of annual cohorts of needles present, averaged from three crown heights on 10 trees per stand, and averaged for the 4 years between 1998 and 2001 (Maguire et al. 2003).

Twelve trees were randomly selected from each stand, with the following restrictions: selected trees were dominant to codominant, at least 20 m apart from one another, and nonforked. In April 2002, each tree was cored to the pith at breast height with a 5-mm increment borer. The cores were divided into heartwood and sapwood segments based on color, and each segment was immediately wrapped in plastic film to prevent moisture loss. Within 12 h the core segments were weighed to the nearest 0.01 g, then oven-dried and reweighed. Moisture content was calculated as 100 × (green mass – dry mass) / dry mass.

The trees were felled between April and June 2002. From each tree, two disks, 5 and 30 cm tall, were cut from the internode at about breast height. In addition to the stand-level needle retention values, needle retention was assessed for three of the felled trees selected at random from each stand. This assessment allowed us to examine tree-level associations with needle retention to a limited extent. On each breast-height disk, total diameter and heartwood diameter were measured to the nearest millimetre on two perpendicular axes; from these measurements, breast-height area and heartwood area were estimated, and sapwood area was calculated as the difference.

From each of the 30-cm sections, eight vertical beams (each 1 cm tangentially, 1 cm radially, and at least 16 cm longitudinally) were cut from around the entire perimeter of the stem so that they contained the outermost wood. The beams were subjected to static bending tests on an Instron™ universal testing machine according to an American Society for Testing and Materials standard D 143-94 (American Society for Testing and Materials 1999), with minor modifications, as follows. The beam supports were set 15 cm apart for a span:depth ratio of 15:1, and the beams were placed so that the load was applied to the tangential face closest to the pith. The load was applied continuously at a rate of 5 mm/min. MOE (stiffness) and MOR (the maximum force withstood before breaking) were then calculated for each beam according to the formulas specified in Markwardt and Wilson (1935); MOE was the slope of the linear portion of the stress/strain curve and MOR was the stress applied at beam failure.

From each of the 5-cm tall breast-height disks, a diametric strip 1.5-cm wide tangentially and 1.5-cm longitudinally was sawn. The strip was located so that it was neither the longest nor the shortest diameter and consisted of clear wood. From one end of this strip (chosen at random), the outermost 2 cm of radial growth was cut and sent to the SilviScan II® facility at CSIRO in Australia. SilviScan II is an automated wood analysis tool that quickly estimates wood density through X-ray densitometry and MFA through X-ray diffraction (Evans and Ilic 2001). Density was estimated at 0.1-mm intervals along the cross-section, and MFA was estimated at 0.2-mm intervals. For each sample, SilviScan provided overall and ring-by-ring values for ring width, earlywood width, latewood width, latewood proportion, ring density, earlywood density, latewood density, earlywood MFA, and latewood MFA.

Because we found that BHage and needle retention were correlated and confounded in the original sample, four additional sites with BHage between 25 and 30 years were sampled in 2003. Needle retention values for these four stands were only available for 1 year (2003) and only for the sixth

Table 1. Descriptions of stands for the main and the supplemental studies and their means for a number of characteristics.

Stand ID	Lat. (°N)	Long. (°W)	Site index	BHage (years)	NR (years)[a]	Basal area (m^2/ha)	MOE (GPa)	MOR (MPa)	Wood density (g/cm^3)	MFA(°)	DBH (cm)	Sapwood moisture content (%)	Sapwood area (cm^2)
Main study													
1	44.687	123.947	38.4	19.0	2.14	29.6	11.5	94.6	0.548	14.2	24.7	87	220
2	45.126	123.644	43.0	19.6	3.03	16.7	13.0	104.8	0.578	12.5	21.3	82	211
3	45.928	123.720	39.3	21.0	2.43	21.1	11.7	99.2	0.543	15.1	28.7	90	257
4	44.626	123.801	39.0	21.1	2.76	19.5	12.2	102.7	0.572	16.7	29.2	86	358
5	45.336	123.747	39.0	22.3	2.55	19.5	11.6	101.4	0.589	15.9	25.2	96	284
6	45.357	123.787	41.7	22.8	2.14	24.6	12.6	105.7	0.604	15.1	25.4	67	249
7	45.432	123.703	41.7	22.8	2.12	18.4	13.5	114.1	0.640	13.5	23.3	71	169
8	45.207	123.849	40.8	23.0	2.65	26.1	12.8	106.8	0.610	14.2	24.3	65	232
9	45.280	123.630	41.2	24.0	2.34	25.3	12.5	102.5	0.562	15.1	28.5	95	264
10	45.676	123.898	42.4	24.7	1.77	39.2	12.4	105.2	0.609	16.2	25.2	74	172
11	45.215	123.796	39.1	24.8	2.40	38.8	12.1	104.5	0.588	16.3	28.6	97	291
12	45.770	123.818	40.0	27.4	1.53	39.3	14.4	116.0	0.649	13.8	28.9	69	291
13	45.621	123.849	41.2	27.6	1.75	37.6	12.9	108.9	0.633	15.1	28.7	69	241
14	45.259	123.889	39.4	27.8	1.61	37.5	14.3	117.9	0.673	14.3	27.6	62	225
15	45.340	123.819	39.3	30.4	1.82	23.4	14.2	120.9	0.664	14.5	31.1	57	307
Supplemental sites													
A	44.597	123.634	41.9	25.5	3.60	13.3	11.4	100.9	0.541	16.7	32.2		
B	44.613	123.661	44.2	26.6	3.76	11.9	11.4	103.1	0.554	17.1	34.8		
C	45.279	123.601	39.3	27.1	3.23	10.5	11.1	100.8	0.513	17.6	33.2		
D	45.291	123.582	44.0	27.8	3.33	14.0	11.6	107.8	0.545	15.5	34.8		

Note: BHage, breast-height age; MOE, modulus of elasticity; MOR, modulus of rupture; MFA, microfibril angle; DBH, diameter at breast height.

[a]Average number of years of foliage cohorts averaged over the years 1998–2001 for the entire crown, except for the supplemental stands, which only had an estimate for a single whorl in 2003 and estimates were adjusted (see text).

whorl. Previous work has shown that this whorl yields needle retention values that are about 0.32 years less than the method used for the 15 plots sampled in 2002 (data not shown). All four stands had adjusted needle retention values that were between 3.2 and 3.8 years of foliage (Table 1). These stands were used for a direct comparison with four stands of similar age (between 26 and 31 years BHage), but that had less needle retention (1.5 to 1.8 years of foliage).

Data analysis

MOE, MOR, rings per centimetre, and ring width (inverse of rings per centimetre) for each of the eight beams per tree were averaged to obtain values for each tree. The SilviScan data were limited to rings that were present in the outer 1 cm of the samples to coincide with the rings that were present in the small beams. The ring widths of the outermost ring were discarded from the analyses because they often had missing wood segments. Earlywood and latewood densities and MFAs were weighted by appropriate ring widths when calculating means. Stand-level averages for these variables, along with BHage, DBH, sapwood area, and sapwood moisture content, were obtained by averaging the values from each of the 12 trees per stand (Table 1). At the among-stand level, we used correlation analysis and multiple regression to examine the association between the 4-year mean of stand needle retention scores and each wood property. Correlations were calculated both as simple correlation coefficients and as partial correlation coefficients after adjusting for stand BHage using the CORR procedure of SAS (SAS 1990). The full regression model took the following form:

$$[1]\quad \text{Wood property} = \text{intercept} + \beta_1 \times \text{BHage} + \beta_2 \times (\text{BHage})^2 + \beta_3 \times (\text{NeedleRetention}) + \beta_4 \times (\text{NeedleRetention})^2$$

Reduced models having fewer independent variables were also evaluated when independent variables were found to be nonsignificant.

We also adjusted for BHage by adjusting individual trees for the average ring age in the beams. The analysis used the individual tree data, except that the needle retention value given each tree was the stand value, because needle retention is a plot-level value. The significance of needle retention was tested against the plot mean square using the appropriate degrees of freedom (df = 1, 12). The model was

$$[2]\quad \text{Wood property} = \text{intercept} + \beta_1 \times (\text{AveRingAge}) + \beta_2 \times (\text{NeedleRetention}) + \text{Plot}_k + \text{error}$$

where Plot_k is the effect of the kth stand and was the error term for testing the effect of needle retention.

The association of needle retention (and rings per centimetre) with wood properties at the tree-within-stand level was examined using random coefficient modeling, using the SAS MIXED procedure (Littell et al. 1996). Random coefficient modeling assumes that the regression model within each stand (e.g., individual tree needle retention vs. a wood property such as MOE) is a random sample from the population of all stands and that each regression model is a random deviation from some population regression model. The analysis then uses the regression models from all the sampled stands to derive an estimate of the "population" regression model, which describes the general within-stand association of needle retention and a wood property for the entire population of Douglas-fir in the study region. The regression coefficients from random coefficient modeling at the within-stand level can be compared with the regression coefficients from simple linear regression at the among-stand scale.

The wood properties of the four "healthy" stands sampled in 2003 (>3 years of needle retention) were compared with four stands severely impacted with SNC (<2 years of needle retention) using a Student's t test, where the stand means were used as the data points.

Results and discussion

Individual tree data

All examined wood properties showed significant differences among stands with associated p values < 0.05. The distribution of variance components among stands and within stands are shown in Table 2. The proportion of variance was relatively high among stands (and, consequently, low within stands) for needle retention and BHage. The proportion of variance was relatively low among stands (and, consequently, high within stands) for DBH, MOE, MOR, earlywood density, earlywood and latewood MFA, and sapwood area. For other variables, the proportion of variance was relatively balanced within and among stands.

The random coefficient modeling found that within stands, needle retention appeared to impact only latewood MFA; trees with higher needle retention had lower latewood MFA (MFA = intercept – 2.69×(latewood MFA), $p < 0.01$). No other variable showed statistical significance at $p = 0.10$. The lack of statistical significance could have been for two reasons: (1) the sample size of three trees per stand gave very little power to detect within-stand associations and (or) (2) the associations within stands were really not there. The individual tree retention values were similar to the 4-year average (1.9 vs 2.2 years), but the stand-level correlations were low (0.16), indicating that 1 year of measurements on three trees was inadequate to represent the stands.

Stand-level data

At the among-stand level, reduced foliage was correlated with increased MOE and MOR. These correlations are probably driven by the negative correlation between needle retention and average ring density, which in turn results from higher latewood proportion (Table 3, 1st column, Figs. 1*a*, 1*b*, 1*c*). Reduced needle retention was also associated with decreased sapwood moisture content, but was not associated with ring MFA.

The simple correlations suggest that needle retention can explain a significant amount of the observed differences in MOE and MOR. However, stand-level needle retention was also correlated with BHage ($r = -0.75$, $p < 0.01$) and basal area per hectare ($r = -0.71$, $p < 0.01$); older stands and stands with more basal area had lower needle retention. Neither of these variables was correlated with needle retention in the full set of 70 permanent plots from which we selected our 15 sample plots. In our attempt to hold site index relatively constant and to sample plots with a wide range of needle retention, we inadvertently forced these correlations. In

Table 2. Stand-level summary data and proportion of the variation attributed to the among-stand, within-stand, and within-tree variance components for 15 stands.

					Variance component		
Variable	Stand mean	Standard deviation	Min.	Max.	Among stands	Within stand	Within tree
Needle retention (years)	2.20	0.47	1.53	3.03	58%	42%	na
DBH (cm)	26.7	2.7	21.3	31.0	18%	82%	na
Breast height age (years)	23.7	2.4	20.5	27.8	89%	11%	na
Rings/cm (outer 1 cm)	4.4	1.3	2.5	7.0	43%	39%	17%
Ring width (mm)	2.5	0.8	1.3	4.4	36%	41%	23%
Earlywood width (mm)	1.24	0.52	0.60	2.29	41%	59%	na
Latewood width (mm)	1.30	0.33	0.74	2.08	31%	69%	na
MOE (GPa)	10.4	0.8	9.3	11.7	10%	46%	44%
MOR (MPa)	99.9	6.8	88.9	112.9	13%	49%	38%
Ring density (g/cm^3)	0.60	0.04	0.52	0.68	29%	55%	16%
Earlywood density (g/cm^3)	0.31	0.02	0.28	0.35	11%	89%	na
Latewood density (g/cm^3)	0.83	0.05	0.74	0.92	46%	54%	na
Earlywood MFA (°)	17.9	1.6	14.9	21.1	10%	90%	na
Latewood MFA (°)	11.9	1.1	9.6	14.1	10%	90%	na
Latewood proportion	0.53	0.05	0.45	0.61	29%	71%	na
Sapwood moisture content (%)	77.9	13.3	56.6	96.9	35%	65%	na
Sapwood area (cm^2)	230.7	39.5	182.6	308.6	16%	84%	na

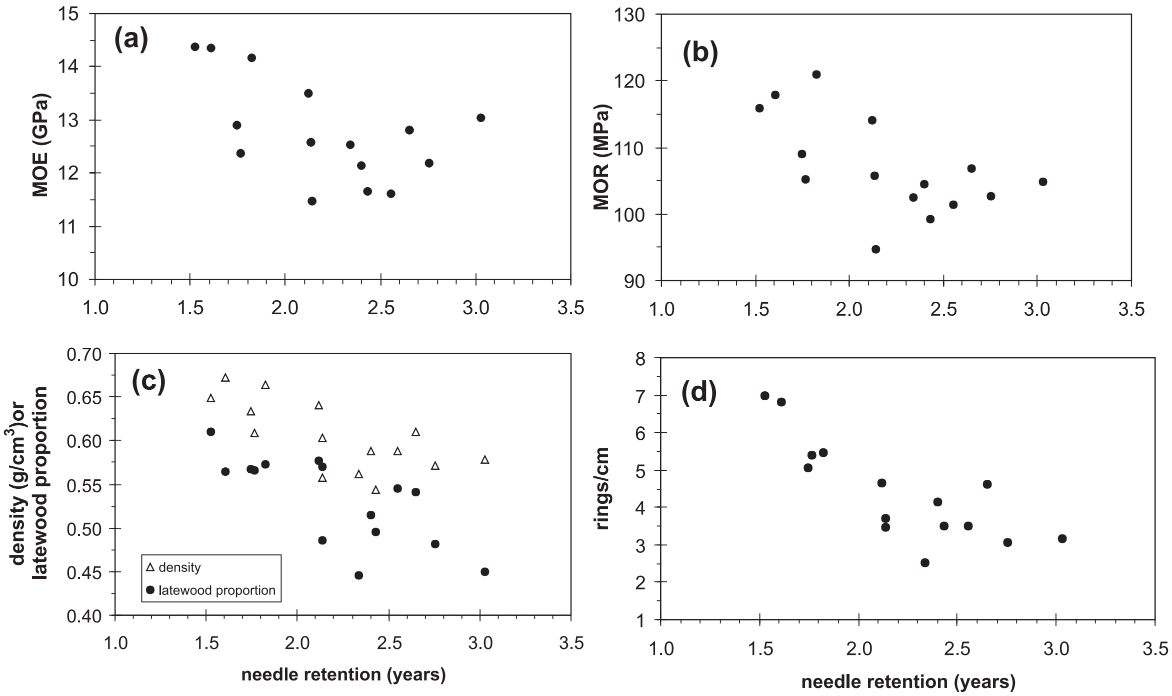
Note: DBH, diameter at breast height; MOE, modulus of elasticity; MOR, modulus of rupture; MFA, microfibril angle; na, not applicable, because we had only one measurement per tree.

Table 3. Correlations of wood properties with needle retention (NR) and breast-height age (BHage).

	Correlations with NR			Correlations with BHage	
Property	*r*	Adjusted for BHage	NR < 2.5 years and adjusted	*r*	Adjusted for retention
BHage	**–0.75**	—	—	**1.00**	
Rings/cm	**–0.80**	**–0.55**	**–0.80**	**0.75**	0.39
Ring width	**0.69**	0.41	**0.58**	**–0.66**	–0.29
Earlywood width	**0.71**	0.42	**0.58**	**–0.68**	–0.32
Latewood width	**0.63**	0.35	**0.55**	**–0.59**	–0.24
MOE	**–0.55**	–0.03	–0.45	**0.72**	**0.56**
MOR	**–0.59**	0.07	–0.26	**0.83**	**0.72**
Density	**–0.68**	–0.17	**–0.57**	**0.82**	**0.65**
Earlywood density	0.31	0.41	0.51	–0.05	0.28
Latewood density	–0.16	0.26	–0.20	0.42	**0.47**
Latewood proportion	**–0.74**	**–0.50**	**–0.62**	**0.65**	0.23
MFA	0.01	0.08	0.42	0.06	0.10
Earlywood MFA	0.06	0.11	**0.58**	0.02	0.10
Latewood MFA	**–0.48**	–0.19	–0.12	**0.50**	0.24
Sapwood moisture content	**0.56**	0.22	**0.63**	**–0.60**	–0.33
Sapwood area	0.17	**0.47**	**0.53**	0.18	**0.47**

Note: Partial correlation coefficients are reported for needle retention adjusted for BHage (for all stands and the 11 stands with needle retention <2.5 years of foliage) and for BHage adjusted for needle retention. Correlations that are statistically significant at $\alpha = 0.10$ are in bold. Correlation coefficients statistically significant at $\alpha = 0.01$ and 0.05 are ±0.64 and ±0.51, respectively, for correlations involving 15 stands, and ±0.73 and ±0.60, respectively, for the 11 stands with needle retention <2.5 years. MOE, modulus of elasticity; MOR, modulus of rupture; MFA, microfibril angle.

Fig. 1. Relationships between needle retention and (*a*) MOE, (*b*) MOR, (*c*) ring density and latewood proportion, and (*d*) rings per centimetre. Each point is the mean for a stand.



our sample, total basal area was not significantly correlated with MOE or MOR (data not shown), but MOE and MOR were more strongly correlated with BHage (r = 0.72 and 0.83, respectively) than with needle retention (r = –0.55 and –0.59, respectively; Table 3).

Even though the trees were at the end of the stage at which they would produce juvenile wood (having BHages of 19–30 years), there can still be subtle changes in properties in Douglas-fir at these ages (Megraw 1986; Abdel-Gadir and Krahmer 1993). Thus, it is not entirely surprising that MOE and MOR were correlated with BHage. The difficulty with the data set is that in choosing from the population of stands with needle-retention history, and keeping in line with our constraints on site index and age, we inadvertently sampled trees in which the older stands had lower needle retention than the younger stands, thus confounding the results. Partial correlation coefficients were used to examine the correlation of needle retention with the wood properties after adjusting for BHage; the same was done for BHage correlations after adjusting for needle retention (Table 3, 2nd and 5th columns). After adjustments, BHage continued to be correlated significantly with MOE and MOR (as expected), but needle retention appeared to impact only rings per centimetre and latewood proportion (at $p < 0.05$).

Partial correlation coefficients are helpful in better understanding relationships when independent variables are correlated, but they cannot completely adjust for colinearity issues. The lack of significance of needle retention on wood properties was surprising because (1) an earlier study had shown a highly significant impact of foliage retention on wood density (Johnson et al. 2003), (2) the difference in latewood proportion should have resulted in a change in wood density, given that neither earlywood nor latewood density was affected, and (3) when individual tree data were used in regression eq. [2], needle retention showed considerably more statistical significance for MOE (p = 0.1037), MOR (p = 0.1178), density (p = 0.0384), and latewood proportion (p = 0.0198).

The quadratic regression model [1] was also used to examine the impact of needle retention and BHage for each of the wood properties. The quadratic term for needle retention was significant only for MOE, yielding the following equation:

$$[3] \qquad \mathrm{MOE} = 19.9 + 0.162 \times (\mathrm{BHAge}) - 9.961 \times (\mathrm{NeedleRetention}) + 2.170 \times (\mathrm{NeedleRetention})^2$$

The R^2 for the model was 0.7048. The inflection point for this equation occurs at the needle retention value of 2.3, implying that the impact of needle retention on MOE is different for stands with <2.3 years of needles than in stands with >2.3 years of needles. In our study population, the lower ranges of needle retention were relatively well sampled, but very few stands (only three) had >2.5 years of needles. Therefore, the relationship between needle retention and MOE in the healthier stands cannot be described well with this data set.

Scatter plots of stand-level needle retention versus MOE or MOR (Figs. 1*a*, 1*b*) showed that as needle retention rose over about 2.5, the negative correlation between retention and MOE or MOR no longer occurred. This trend was also apparent in the significance of the quadratic regression model for MOE incorporating the squared needle-retention term.

Because the relationship between MOE and needle retention was most evident in the stands with less foliage, we also examined the relationships between needle retention and the wood properties for the 11 stands with <2.5 years of foliage (Table 3, 3rd column). In these stands, it appeared that needle retention could possibly be having an impact on many wood properties, but not MOR, latewood density, or late-

Table 4. Means and standard error of four healthy stands (needle retention >3 years) sampled in 2003 and four stands impacted by Swiss needle cast (needle retention <2 years) sampled in 2002, with the probability level that the two populations differ.

	Healthy stands		SNC stands		
Property	Mean	SE	Mean	SE	$p > t$
Breast-height age (years)	26.7	0.5	28.3	0.7	0.12
Rings/cm	3.9	0.4	6.1	0.5	0.01
Ring width (mm)	3.15	0.30	1.62	0.13	<0.01
Earlywood width (mm)	1.74	0.19	0.69	0.05	<0.01
Latewood width (mm)	1.31	0.12	0.93	0.08	0.04
MOE (GPa)	11.5	0.06	14.0	0.35	<0.01
MOR (MPa)	105.1	1.83	115.9	2.55	0.01
Density (g/cm^3)	0.546	0.003	0.655	0.009	<0.01
Earlywood density (g/cm^3)	0.300	0.004	0.298	0.006	0.79
Latewood density (g/cm^3)	0.811	0.013	0.873	0.022	0.05
MFA (°)	16.2	0.38	14.4	0.27	<0.01
Earlywood MFA (°)	18.4	0.49	17.8	0.33	0.32
Latewood MFA (°)	13.0	0.04	12.2	0.19	<0.01
Latewood proportion	0.42	0.013	0.58	0.008	<0.01

Note: MOE, modulus of elasticity; MOR, modulus of rupture; MFA, microfibril angle.

wood MFA (all of which had adjusted r values of ±0.26 or less). Thus it appears that latewood quality — its density and MFA — are unaffected by needle retention, but latewood proportion is.

Because the impact of needle retention was in question due to colinearity issues (see previous text), we sampled four additional stands in the Oregon Coast Range that had >3 years of foliage retention with BHages between 25 and 30 years. We could then compare these four stands with the four oldest stands in our original sample (stands 12–15). We compared older stands to avoid the juvenile core of the trees as much as possible. The average needle retention values were 1.7 years of foliage for the original four stands and 3.5 years (after adjustment) for the additional four stands.

The four SNC-impacted stands had narrower ring width and higher values of MOE and MOR than the healthy stands (Table 4). Moreover, the SNC-impacted stands had higher latewood proportion and wood density and lower MFA than the healthy stands. These results suggest that SNC is indeed associated with wood that has higher density, higher latewood proportion, and higher MOE and MOR than healthy stands.

The increased values of MOE and MOR associated with low needle retention are probably the result of an increase in wood density and decrease in MFA (Tables 3 and 4). Because latewood has over twice the density and two-thirds the MFA of earlywood (Tables 1 and 4), an increase in proportion of latewood will result in higher density and lower MFA. Thus, the increased latewood proportion appears to be the primary reason for increased MOE and MOR in stands with poor needle retention. When considering the pattern of needle growth and loss in SNC-infected trees, this is logical. SNC causes older cohorts of needles to fall prematurely; these needles generally drop in the winter (Manter et al. 2003; Weiskittel 2003). Thus, the tree is deprived of photosynthetically active surface in the early growing season, before the current-year's needles have fully developed and when earlywood is produced. By the time the tree has begun to produce latewood, the current-year's needles are developed, and thus the tree has more available photosynthate than in spring. As a result, a greater proportion of the annual ring is made up of latewood than would normally occur in a healthy tree. The increased latewood proportion in infected stands would also explain the observed reduction in sapwood moisture content.

Growth rate effects on MOE and MOR

Of particular interest is the relationship between ring width and needle retention. Trees infected with SNC have reduced growth as evidenced by the strong negative correlation between needle retention and rings per centimetre (Table 3, Fig. 1*d*). The wood properties are more strongly correlated with rings per centimetre than with ring width, suggesting a curvilinear relationship with ring width (data not shown). Therefore, we present the data for rings per centimetre, rather than ring width, although one is highly correlated with the other (r = –0.89). At the stand level, we found a strong association between ring width (or rings per centimetre) and several ring properties, including ring density and latewood proportion (Table 5, Fig. 2*a*). As with needle retention, we also ran the random coefficient model to better understand the relationship between rings per centimetre and wood properties within a stand. Because all trees had estimates of rings per centimetre, we could produce a model with the full set of 179 trees. In both the stand-level and trees-within-stand models, the increase in ring density with decreasing ring width (increasing rings per centimetre) was a function of the increasing latewood proportion (Table 5). Although at the stand level no relationship was found between any MFA component and ring width, at the tree level earlywood MFA increased with ring width, resulting in increased overall MFA with increasing ring width. There was also a weak association between ring width and latewood density, with narrower rings linked to higher density. Because increased density and lower MFA contribute to higher wood strength and stiffness, we also found increasing MOE and MOR with decreased ring width at both the stand and tree level (Table 5, Fig. 2*b*).

Table 5. Correlation coefficients (r), partial correlation coefficients (r_{adj}) adjusted for breast-height age, and regression coefficients (b) for the relationship between rings per centimetre and wood properties.

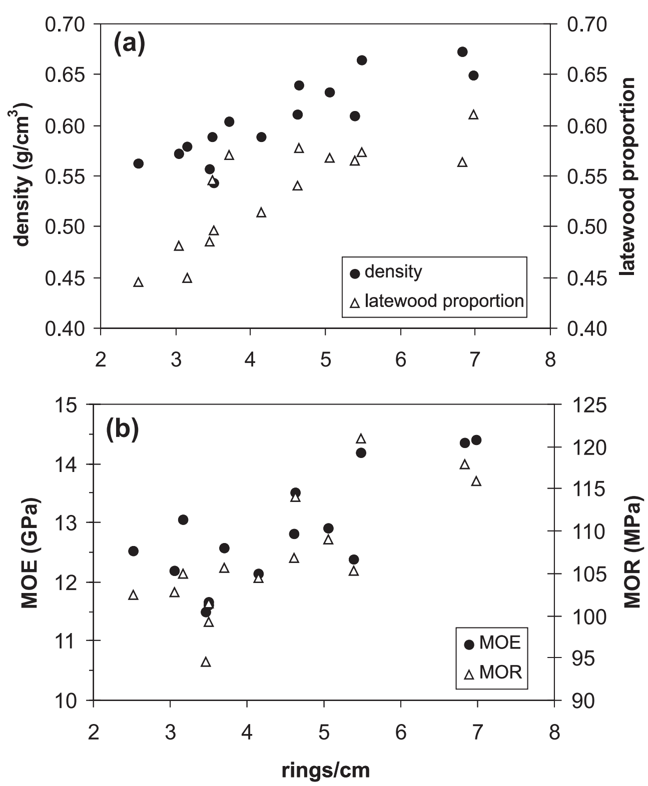
		Stand level (n = 15)			Tree level (n = 179)	
Property	r_{adj}	r	b	$p > F$	b	$p > F$
MOE	0.49	0.77	0.448	<0.01	0.523	<0.01
MOR	0.45	0.79	2.10[a]	0.11[a]	3.24[a]	<0.01[a]
Density	0.65	0.86	0.02[a]	0.02[a]	0.02	<0.01
Earlywood density	–0.32	0.02	0.16	0.96	–3.47	0.17
Latewood density	0.00	0.29	10.98	0.29	10.0	0.02
MFA	–0.38	–0.25	–0.21	0.37	–0.64[a]	0.02[a]
Earlywood MFA[b]	–0.43	–0.40	–0.46	0.14	–0.94[a]	<0.01[a]
Latewood MFA	–0.06	0.44	0.37	0.10	–0.04[a]	0.82[a]
Latewood prop.	0.53	0.81	0.03	<0.01	0.023	<0.01
Sapwood moisture content	–0.50	–0.72	–7.10	<0.01	–4.93[a]	0.01[a]
Sapwood area	–0.44	–0.29	–8.47	0.30	–44.3[a]	<0.01[a]

Note: Linear regression coefficients (b) for rings per centimetre at the stand level are reported for the simple model only including rings per centimetre, unless noted otherwise. Correlation coefficients and regression coefficients from random coefficient modeling are reported for the tree-level data. MOE, modulus of elasticity; MOR, modulus of rupture; MFA, microfibril angle.

[a]Breast-height age was significant at p = 0.10 and included in the regression model with rings per centimetre Probabilities are for the partial correlation coefficients and the rings per centimetre regression coefficient in the two-variable model.

[b]The regressions did not converge with Proc MIXED; used Proc GLM.

Fig. 2. Relationships between rings per centimetre and (a) ring density and latewood proportion and (b) MOE and MOR. Each point is the mean for a stand.



These results imply that faster growing Douglas-fir trees produce wood with lower MOE and MOR than do slower growing trees. However, in the present study we only examined trees that were infected with SNC and tried to hold site index fairly constant. Within the scope of this study it was not possible to separate the effects of growth rate and SNC on wood properties. Studies in the literature examining the relationship between growth rate and wood density have yielded mixed conclusions (reviewed in Zobel and van Buijtenen 1989). Many early studies reported that fast-grown trees produced inferior wood; however, these studies may have confounded growth-rate effects with juvenile-wood effects (Megraw 1986).

The next phase of our research involves determining whether the trends reported here are also present in healthy stands. By looking at the relationships between needle retention, ring width, and wood properties in healthy stands and combining the results with the results of the present study, we will be better able to determine whether SNC affects ring properties differently than slow growth in general.

Conclusions

Trees in stands heavily infected by Swiss needle cast have higher MOE and MOR compared with trees in stands with moderate disease levels, and this appears to be mainly a function of increased latewood proportion. These effects are correlated with a decrease in ring width as a result of the disease. As stand-level needle retention increased above 2.5 years, MOE and MOR levels no longer decreased. Within a stand, there was no association between needle retention of individual trees and MOE or MOR.

Because of the close association between needle retention and ring width, it is difficult to separate the effects of the disease from possible growth-rate effects. Similarly, tree age affected MOE and MOR, further confounding the disease effect.

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