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The interactive effect of root disease and climate on wood properties in halfsibling Douglas-fir families

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ABSTRACT

Certain tree phenotypes enhance wood value properties and promote adaptation to climate extremes. However, the disciplines of wood science, physiology, and pathology rarely intersect to elucidate how survival, productivity, and wood property traits relate. Reaction to biotic and abiotic stress agents expressed in trees as disease resistance or tolerance were studied at the cell and tissue level. Five field-grown 21–22-year-old maternal halfsibling Douglas-fir *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco families were inoculated with *Armillaria ostoyae* (Romagn.) Herink to determine the interaction between disease, climate, and family on wood properties obtained from cores. The families originated from a lower elevation ecosystem and were categorized a priori as fungal disease resistant, tolerant or susceptible from a field study. Cell property changes suggestive of hydraulic adaptation to low precipitation were similar but lesser than the changes resulting from fungal root infection. The greatest increase in wood density occurred in disease resistant families after infection through a combination of thicker cell walls, smaller tracheid radial diameter, and reduced earlywood width. Microfibril angle and modulus of elasticity were affected differently with respect to changes in atmospheric relative humidity. Disease resistant compared to susceptible and tolerant families had inherent differences regardless of infection status. The sudden and localized changes in wood density associated with a disease resistance response could negatively impact on product quality, uniformity, and growth; on the other hand, denser wood and reduced growth associated with disease resistance may enhance drought survival. Understanding the interaction of these traits is important for adaptation to environmental stressors.

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1. Introduction

The effects of climate on wood formation have been studied for some time, but there is little information on how disease affects wood quantity or quality even though most trees cope with disease through part or all of their lifespans. This is surprising since disease is defined as an agent that leads to malfunctioning host cells or tissues upon continuous irritation by a pathogenic agent or environmental factor leading to symptomology (Agrios, 2005). In essence, the concept of disease covers a very wide range of biotic and abiotic factors affecting how plants grow and cope with stress. For example in Douglas-fir, Swiss needle cast increased wood stiffness through higher percentage of latewood (Johnson et al., 2005), and Armillaria root disease increased lumber warping caused by differing longitudinal shrinkage (Cruickshank, 2010). Also in Douglas-fir, Martinez-Meier et al. (2009) showed that heritable plasticity in tracheid allometry had a genetic basis for tolerance to drought stress. Further in Douglas-fir, Cruickshank and Jaquish (2014) illustrated a heritable plasticity for resistance or tolerance to Armillaria root disease. These disease studies highlight the induced responses to biotic and abiotic stress in Douglas-fir that may affect wood quality.

Plants generally respond to disease in well-known patterns. Plants either have lower survival relative to other plants (called susceptible) or they survive by either limiting damage from a stress agent (called resistance), or they survive and have superior growth relative to other plants for a given damage level (called tolerance, Schafer, 1971). Both survival mechanisms have costs and benefits and facilitate survival. The concept of resistance or tolerance can be potentially applied to any trait that confers a fitness advantage to individuals in a population under changing environmental conditions (biotic and abiotic). Since resistance or tolerance concepts also apply to climate factors affecting plants and on wood quality, it will be useful to understand how response to a fungal disease agent might also coincide with abiotic responses.

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In conifers, 90–95% of the woody tissue xylem is composed of tracheids. Wood originates in four main steps by the activity of the cambium: cell division, cell expansion, secondary cell wall formation, and then programmed cell death to form the mature tracheid (reviewed by Mauriat et al., 2014). Tracheids link vertically through bordered pits in the cell membrane to form the bulk of the vascular system. The bordered pits are formed first in the primary cell membrane, and then secondary cell wall deposition of polysaccharide microfibrils are wrapped around the primary membrane at an angle to form three distinct secondary cell wall layers. Wood density and strength are linked to the lignification of the secondary cell wall, the wall thickness, and tracheid size. Low microfibril angle relative to the cell axis increases the stiffness of the cell wall and this plus the proportion of latewood affects the modulus of elasticity of the wood and shrinkage after drying (Barnett and Jeronimidis, 2003).

The biological precepts of tree growth govern the variation in wood quality traits because seasonal climate corresponds with cambial activity and cell formation (Antonova and Stasova, 1997). For conifers in temperate climates, after a period of winter dormancy and chilling, the cambium reawakens to produce new xylem composed of large thin walled earlywood tracheids having high conductivity. Later growing season weather promotes the production of latewood consisting of smaller diameter thick-walled latewood tracheids having reduced conductivity but higher mechanical strength. Climate affects the amount of earlywood and latewood within annual rings which then determines wood quality attributes (Shmulsky and Jones, 2011). The differences in earlywood and latewood properties are largely reflected in the differences in tracheid diameter, length, thickness, microfibril angle, and the anabolism of cellulose and lignin (Barnett and Jeronimidis, 2003).

In this study we artificially infected Douglas-fir under field conditions to determine the wood properties of intra annual tree rings. The study objectives were to determine: (i) the effect of climate, (ii) the effect of fungal root disease, and (iii) how differences at population and the halfsibling levels determine response to climate and disease. Annual climate conditions were assigned to individual tree ring wood properties before and after inoculation and in control trees. Douglas-fir halfsibling families were identified previously (Cruickshank et al., 2010) based on survival to Armillaria root disease, and in a subsequent study (Cruickshank and Jaquish, 2014) for disease resistance and tolerance. The differences in these pathological strategies and their interaction with climate and wood quality are reported for five halfsibling families. There is a lack of information on how climatic factors interact with biotic disease to affect wood quality and what role conifer genetics may play in this interaction.

2. Materials and methods

2.1. Inoculum production

Inoculum units were prepared at the Canadian Forest Service, Pacific Forestry Centre, Victoria, BC from freshly cut 1.5 kg blocks of 15–25-year-old paper birch (*Betula papyrifera* Marsh.) harvested from the BC interior. The inoculum production is described in detail in Cruickshank and Jaquish (2014), and briefly summarized as follows. Blocks were autoclaved in autoclave bags and then aseptically inoculated with *Armillaria ostoyae* and placed in plastic storage boxes for 2-year colonization. After colonization, a living Garry oak branch segment (*Quercus garryana* Douglas) was inserted tightly into a hole drilled perpendicular in one cut end of each block. The inoculum units were then stored in moist sand-filled plastic bins until the oak branch cambium became either colonized. The units were then transported to the BC Ministry of Forests, Lands and Natural Resource Operations Interior Douglas-fir progeny test near Duncan Lake, BC.

2.2. The test site and tree inoculation

The progeny trial near Duncan Lake (lat. 50°21′57.3″N, long. 1 16°54′45.4″W, elevation 640 m) is a gently sloping site with a southwest aspect situated in the Interior Cedar-Hemlock biogeoclimatic ecosystem (Meidinger and Pojar, 1991). The test was planted in 1987 with wind-pollinated *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco seedlings families from the West Kootenay low elevation seed planning zone (see Cruickshank and Jaquish, 2014 for site layout and tree summaries). Biologically, these seed zones are surrogates for the physical environment in which seedlings grow to their genetic potential, and moving beyond these areas usually results in maladaptation (Ying and Yanchuk, 2006). The Douglas-fir families were identified from a greenhouse challenge of the families to *A. ostoyae* and chosen to cover a range of 3-year seeding survival: family 421 (12%), 422 (47%) 423 (35%) 514 (7%) and 620 (44%) (Cruickshank et al., 2010). A field study of the same families was conducted (outlined in Cruickshank and Jaquish, 2014) in which inoculum units were placed in 2004 for families 421 and 423 and 2005 for families 422, 521, and 620. The trees were left until 2009 when the roots of these and healthy trees of the same families were excavated and examined for lesions. From this study the separation of trees based on susceptible, resistant, or tolerant designations were completed (Cruickshank and Jaquish, 2014). Findings from both previous studies are briefly summarized as follows. Families 421 and 514 with low seedling study survival and large lesion size in the field study were deemed susceptible. Family 423 with good seedling survival, and large lesions coupled with superior infected tree growth in field studies was deemed tolerant. Families 422 and 620 both had good seedling survival and small lesions but resulted in reduced infected tree growth in field studies and were deemed resistant. Family 422 was the most resistant and had the smallest lesion size followed by family 620.

The progeny trial is located in the ecosystem where Armillaria root disease does its most damage but the fungus is not strongly affected by climate except for more extreme conditions (Cruickshank, 2016). Damage from Armillaria root disease consists of volume growth reduction in planted Douglas-fir sites of approximately 10% by age 30 (Cruickshank et al., 2011), and mortality in undisturbed stands at up to 40% by age 90 (Cruickshank, 2016).

2.3. Wood property sampling and analysis

In 2009, only trees with successful fungal inoculum transfer to the tree root and healthy trees were sampled for one core per tree at 1.3 m using a 12 mm increment borer (Table 1). The cores were dried and sent to FPInnovations in Vancouver, BC for wood property scans using Silviscan (69 trees total-Table 1). Each core was scanned for radial and tangential fiber dimensions using optical

Table 1
Number of cores taken from field trees for wood property analysis, and year inoculated.

Family	Healthy	Infected	Total	Year inoculated
421	5	7	12	2003
422	5	8	13	2004
423	6	9	15	2003
514	9	7	16	2004
620	6	7	13	2004
Total	31	38	69	

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