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The interaction between competition in interior Douglas-fir plantations and disease caused by *Armillaria ostoyae* in British Columbia

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ABSTRACT

Interior Douglas-fir trees in plantations were assessed for size differences related to the level of diseased neighbours infected with *Armillaria ostoyae*. The four Douglas-fir stands studied ranged from 25- to 34-year-old, and represented the oldest accessible planted stands in the Interior Cedar Hemlock (ICH) ecosystem in British Columbia. Twenty-three to 25, 10-m radius plots were established in each stand. The spatial coordinates, total height, and diameter at breast height of all live and dead trees in the plots were recorded. Subject trees whose competitors were contained in the 10-m radius plots were also identified. Trees were pulled out of the soil using a mechanical excavator and the root systems were surveyed for evidence of infection by *A. ostoyae*. Stem disks were taken from each tree at 1.3 m above the ground for a determination of basal area. Increasing proportion of diseased trees in the plots resulted in less total plot basal area, but did not affect the mean basal area or height. Individual subject tree basal area was negatively related to the level of disease in surrounding competitors, opposite to expectations; however, diseased subject trees had reduced height and basal area compared to disease-free subject trees. Increasing competition reduced both the height and basal area of the trees, while regular distribution of all trees increased both total and mean plot basal area but not height. Disease incidence at the plot level and in individual subject trees was mainly affected by the neighbourhood conditions in which it grew, and was also related to disease intensity in the tree root systems. Although disease may alter resource partitioning among trees, the utilization of these resources is mostly limited by the increasing disease incidence as the stands age, the higher probability of larger trees being diseased with time, the occurrence of dead trees in clumps, and the high probability that dead trees will eventually infect live neighbours. The widespread belowground incidence of *A. ostoyae* in the ICH, its rapid colonization of stumps, and its wide host range can reduce site potential in managed stands.

1. Introduction

Information concerning impact of pests in managed and unmanaged areas is used to allocate resources to control pests, to determine treatment thresholds, and to calculate the economic impact and risk of pests for industrial, ecological, and social concerns. Losses due to pests are usually determined as a damage function relating percent loss to the level of pest damage (Walker, 1983). The damage function is critical for determining thresholds for control and for calculating economic impacts. One factor that can affect the shape of the damage function is the ability of surviving plants to compensate for losses by increased growth. Compensation growth can occur as regrowth of damaged individuals such as after browsing, but more commonly with insects and disease this occurs at the neighbourhood level due to changes in competitive interference.

Competition is usually defined as the reciprocal negative interactions between two organisms, but can also include apparent competition where two species interact through a shared enemy or where different species interact through multiple plant species (Connell, 2003). Competition can exert its effect in a population through changes in resource availability or the ability to tolerate changes in resources. Disease can affect plant competition by changing the way resources are partitioned among individuals. Disease-free plants may have competitive advantage if resources become available because of their infected or dead neighbours. The effect of disease on site productivity may not represent a simple loss of growth in diseased plants if healthy neighbours can compensate for some losses.

Compensation growth has been recognized in agricultural settings for some time (Kirkpatrick and Blodgett, 1943; de Wit, 1960). More recently studies have reported that disease-free annual

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plants were able to compensate for yield losses in diseased neighbours (Adams and Lapwood, 1983; Friess and Maillet, 1996; Mihail et al., 1998), but plants weakened by infection are not always able to compensate for the reduced growth of infected neighbours (Adams and Lapwood, 1983). In mixed stands of Douglas-fir [*Pseudotsuga menziesii* var. glauca (Beissn.) Franco] and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia Engelm.), growth of Douglas-fir increased after the pine was attacked by insects (Heath and Alfaro, 1990). Similarly, growth efficiency of disease-free trees in stands affected by Phellinus root disease increased compared to a stand with no disease (Oren et al., 1985). Disease-free trees in stands with Annosus root disease had no additional growth associated with diseased neighbours (Bendz-Hellgren and Stenlid, 1997).

Armillaria ostoyae (Romagn.) Herink causes Armillaria root disease of conifers in western North America (Wargo and Shaw, 1985; Kile et al., 1991). The fungus is widespread in the northern hemisphere, and can infect most tree species (Kile et al., 1991). In the southern interior of British Columbia (BC), Armillaria root disease is found in most biogeoclimatic zones (Braumandl and Curran, 1992; Lloyd et al., 1990), but is most problematic in the Interior Cedar Hemlock (ICH) biogeoclimatic zone. The ICH zone is second only to the Coastal Western Hemlock zone in productivity within BC and Canada and has the highest diversity of tree species within BC (Meidinger and Pojar, 1991). The incidence of infection increases slowly over time and causes mortality and understocked openings, with a peak in mortality around stand age 15–20 (Morrison and Pellow, 1994). Since the fungus spreads slowly via root to root contact and rhizomorphs in the soil, only some trees are infected at any one time (Morrison et al., 2000) and only a smaller percentage of these actually die from an initial infection (Cruickshank et al., 1997; Morrison et al., 2000). By stand age 30, this results in a mix of dead trees, living diseased trees, and disease-free trees in stands (Morrison et al., 2000). Inoculum is long-lived, and may survive for decades in stumps (Roth et al., 1980).

Many interior Douglas-fir plantations have been established over the last 40 years in the southern interior of BC where the impacts of the disease are not well known. Losses in growth and mortality may be overestimated if disease-free trees can compensate for some of the production loss in diseased neighbours. Infected mature interior Douglas-fir trees suffer mortality and reduced growth after infection (Bloomberg and Morrison, 1989), but disease-free trees may be released from competitive interference by dead and diseased neighbours. The current study addresses the hypothesis that disease in interior Douglas-fir can alter intraspecific tree interactions. This was tested in individual trees (subject trees) and in groups of disease-free trees growing in neighbourhoods with varying disease incidence.

2. Materials and methods

2.1. Sites, plot locations, and tree measurements

Four, 25- to 34-year-old Douglas-fir plantations in south-central BC (in the ICH biogeoclimatic zone) were identified for sampling. Separated by at least 50 km, these sites were located at Chuck Creek (CC) near Clearwater, East Barriere (EB) near Barriere, Kingfisher (KF) near Enderby, and Kuskanax (KX) near Nakusp (Table 1). Site selection was limited to areas with access roads that would accept a lowbed trailer carrying a 20-ton excavator, and to areas that would permit excavator travel on site. Three sites (CC, EB, and KF) were previously clearcut and then planted with interior Douglas-fir, the other site (KX) was planted after a wildfire. For each site 10-m radius plots (0.03 ha) were randomly distributed throughout the site on either side of the main access road, except where excavator travel would not permit and the plots had to be moved locally. In almost all plots, EB had slightly greater proportion of other tree species (20%) mainly as naturally regenerated spruce (*Picea* spp.) and aspen (*Populus* spp.) species (Table 1). The chosen sites had low to moderate disease incidence for this ecosystem based on a walkthrough survey.

In each plot, all dead and living trees were tagged and the diameter at 1.3 m (breast height) and total height were recorded by species. The horizontal distance from the plot center to the center of each tree was measured with a tape measure, and the azimuth between the north line and the tree in question was measured using a survey transit. Douglas-fir subject trees (median 4 per plot) were identified so that all of their competitor trees were located within the 10-m radius plots. Competitor trees were trees of any species with height exceeding a projected 60° angle from the horizontal and originating at the base of the subject tree (Biging and Dobbertin, 1992); the competitor trees associated with a particular subject tree comprise that subject tree's neighbourhood.

All trees in every plot were pulled out of the soil in the late fall using a 20-ton Link Belt excavator with a clamshell bucket attachment to minimize the breakage of roots, stems and branches. Pulled trees were gently laid on the ground and left in the plot over winter. After the soil thawed the following spring, the soil was removed from the roots of all trees. Lesions caused by *A. ostoyae* were identified on all roots and confirmed by observing mycelial fans in the bark or cambium (of the lesions) or as mycelial fan impressions in or under the bark of older lesions. The proportion of diseased primary roots (>15 mm diameter arising from collar) was recorded for each tree except at site EB.

Cross-sectional stem disks were cut using a chainsaw from all trees at 1.3 m above the soil line and at the soil line (0 m) for all dead trees. The age of the dead trees was determined by counting annual growth rings on the 0 m disks. Very small trees with

Table 1
Site characteristics from 0.3 ha plots at the four study sites: Chuck Creek (CC), East Barriere (EB), Kingfisher (KF), and Kuskanax (KX).

	Site			
	CC	EB	KF	KX
Tree age at sampling (year)	34	25	30	32
Number of plots	25	23	25	25
Median DBH (cm)[a]	15.2 (17.8, 9.7)	12.2 (13.6, 8.1)	14.6 (16.2, 10.7)	16.2 (17.3, 12.0)
Median number of live and dead stems[b]	33 (48, 19)	44 (72, 31)	39 (55, 26)	39 (53, 21)
Proportion of Douglas-fir[b]	0.89 (1, 0.77)	0.80 (0.97, 0.69)	0.86 (1, 0.69)	0.94 (1, 0.78)
Lat/long	51.6N, 119.8E	51.3N, 119.7E	50.7N, 118.7E	50.2N, 117.7E
Proportion of dead trees[b]	0.04 (0.25, 0)	0.04 (0.13, 0)	0.06 0.24, 0)	0.03 (0.09, 0)
Mean tree age at death (year)	28	20	22	22
Proportion of belowground of *Armillaria ostoyae* infected trees[b]	0.35 (0.68, 0)	0.33 (0.51, 0.14)	0.53 (0.87, 0.19)	0.56 (0.85, 0.28)

[a] Values in parentheses are maximum and minimum values.
[b] Values in parentheses are maximum and minimum values for plots.