



Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling

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ABSTRACT

The recent mountain pine beetle outbreak in North American lodgepole pine forests demonstrates the importance of insect related disturbances in changing forest structure and ecosystem processes. Phloem feeding by beetles disrupts transport of photosynthate from tree canopies and fungi introduced to the tree's vascular system by the bark beetles inhibit water transport from roots to canopy; the implications of these processes for tree mortality are poorly understood. We hypothesized that the fungus must quickly disrupt tree water relations because phloem girdling, reported in other studies, requires much longer than a year to cause mortality. We tested the hypothesis in lodgepole pine (*Pinus contorta*) by comparing tree water use, foliar expansion and seasonal variation in predawn water potential on 8 mechanically girdled trees, 10 control trees and 17 trees attacked by mountain pine beetle (*Dendroctonus ponderosae*). Transpiration began to decline within ten days of beetle infestation; two months later, pre-dawn water potential had also dropped significantly as water transport to the canopy declined by 60% relative to healthy trees. There was no water transport or foliar expansion by beetle-infested trees the following year. Experimentally girdled trees continued to transpire, maintain leaf water potential and grow new foliage similar to healthy trees. Our data suggest that fungi introduced by bark beetles in this study are the primary cause of tree mortality following mountain pine beetle attack and significantly reduce transpiration soon after beetle infestation. Rapid decline and the eventual cessation of water uptake by infected trees have important implications for water and nutrient cycling in beetle impacted forests.

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1. Introduction

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) coevolved with conifer species and has been an important disturbance agent in North American pine forests for thousands of years. A number of abiotic and biotic factors typically maintain populations at endemic thresholds (Raffa et al., 2008). At low population levels, bark beetles usually attack stressed trees creating openings in forest stands that allow tree regeneration and dead trees to serve as habitat for wildlife. However, during the past decade and a half, mountain pine beetles are causing significant mortality in millions of hectares of lodgepole pine forests that extend from western Canada to the southern Rockies. The abundance of over mature stands, recent drought and warming winter temperatures has created conditions that support the current outbreak (Raffa et al., 2008). The possibility of further infestations are likely as beetles move into alternate hosts such as jack pine (*Pinus banksiana*) in the boreal forests of North America, and ponderosa pine (*Pinus ponderosae*) in

more temperate forests (Safranyik et al., 2010; Rice et al., 2007; Cullingham et al., 2011).

Bark beetles disrupt two basic life-sustaining transport processes trees they infest. Adult beetles consume phloem tissue in to build egg galleries and developing larvae consume phloem for food until maturity. Together, phloem feeding by adult and larval beetles contribute to some amount of phloem girdling, disrupting the transport of photosynthate from the canopy to other tissues within the tree. Bark beetles also carry a diversity of spores from four main genera of fungi, *Ophiostoma*, *Ceratocystiopsis*, *Grosmannia* and *Ceratocystis* (Six and Wingfield, 2011) and a number of species in these groups have been shown to be phytopathogenic (Christiansen and Solheim, 1990; Yamaoka et al., 1995; Kim et al., 2008). Once inside the tree, fungal spores introduced by bark beetles germinate and the spreading fungal hyphae penetrate water conducting xylem tissue in the sapwood and block water transport from the soil to the canopy (e.g. Ballard et al., 1984; Langstrom et al., 1993; Wullschlegel et al., 2004).

Both fungal infection of xylem tissue and phloem feeding by bark beetles have the potential to cause tree mortality. The link between phloem consumption by bark beetles and tree mortality has not been established, but mechanical girdling has been used to

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examine tree and ecosystem carbon dynamics. In these studies, girdled trees typically live for at least a growing season and often longer before succumbing to the girdle treatment (Scott-Denton et al., 2006; Weintraub et al., 2007; Domec and Pruyn, 2008; Chen et al., 2010). In contrast, experiments that inoculate trees with blue-stain fungi or that measured a transpiration response following beetle infestation suggest that the fungal infection kills trees relatively quickly (Yamaoka et al., 1995; Wullschleger et al., 2004). Although bark beetle fungal associates may not necessarily support bark beetles in overwhelming tree defenses (Six and Wingfield, 2011) the above studies suggest that disruption of photosynthate transport from the canopy and fungal infection of xylem tissue may not be equal players in the eventual mortality of trees following mountain pine beetle infestation.

In spite of the importance of mountain pine beetle to the ecology of North American pine forests, there has never been a study that attempted to simultaneously quantify changes in tree physiology induced by phloem feeding and fungal infection. Several studies have examined changes in transpiration rates following pine beetle infestations or inoculations with blue-stain fungi (e.g. Yamaoka et al., 1990; Wullschleger et al., 2004) while others have examined competitive interactions of different beetle species on phloem consumption, or attack densities of beetles relative to phloem carbohydrate concentrations (e.g. Miller and Berryman, 1986). Understanding the mechanisms behind tree mortality following beetle attack is important for development of control strategies as well as how the timing of mortality in trees and stands affects other ecosystem processes. Our goal in this study was to compare changes in water status and foliar growth of healthy trees, trees girdled to disrupt phloem transport, and trees attacked by bark beetles and blue stain fungi. To accomplish this, we mechanically removed phloem from the entire circumference of healthy trees to simulate severe phloem feeding by bark beetles and compared transpiration, pre-dawn leaf water potential, leaf expansion and foliar nitrogen concentrations with beetle attacked and healthy trees over most of two growing seasons. We hypothesized that tree mortality would occur more quickly in beetle attacked trees compared to girdled trees. Based on this hypothesis, we tested the prediction that a decline in plant water status (as measured by sap flux density measurements, and pre-dawn leaf water potential) leads to drought related tree death in beetle attacked trees while girdled trees maintain a plant water status similar to controls following attack and live for a significantly longer time period compared to beetle infested trees.

2. Methods

2.1. Study site

Our study site was located at the USDA Forest Service's Fraser Experimental Forest (FEF) near Fraser Colorado, USA, (39°4'N 105°52'W). Average annual temperature at FEF is 1 °C, ranging between −40 °C and 32 °C annually while growing season (May–September) temperatures average approximately 10 °C. The forest receives an average of 740 mm precipitation each year, with approximately two-thirds falling as snow. Initial signs of the current mountain pine beetle (MPB) epidemic appeared in 2003 and by 2006 beetles were infesting large numbers of lodgepole pine trees in all of the watersheds at FEF.

2.2. Treatments

In 2006, we located an area within the experimental forest boundary that had experienced bark beetle activity the previous year but where there were still multiple unaffected trees. In early

July 2006, we identified 36 lodgepole pine trees within a 30 m radius that showed no evidence of beetle activity and began monitoring sap flux density on each tree using Granier style sap flow probes (see details below). Treatment trees had an average diameter of 24.0 cm (± 0.54 se) averaged 15.5 m (± 0.3 se) in height and had similar sapwood to leaf area ratios ($0.080 \text{ cm}^2 \text{ m}^{-2} \pm 0.001$ se). We randomly selected 24 of the 36 trees for the control and girdled treatments and sprayed the stems of these trees with a wide spectrum carbamate insecticide (SEVIN, Garden Tech Inc.) to protect them against beetle attack. The insecticide was applied according to the manufacture's recommendation and care was taken not to excessively spray foliage.

Bark beetle emergence began on July 17, 2006 within our study area and by July 19 bark beetles had attacked eighteen of the treatment trees (including seven sprayed trees), as indicated by the presence of abundant pitch tubes and boring dust on the ground, which are indicative of successful infestation. Consequently, we adjusted our sample size for each treatment by randomly selecting non-attacked trees for the control ($n = 10$) and girdle ($n = 8$) treatments and assigned the attacked trees to the beetle treatment ($n = 17$). The girdled treatment was implemented late in the afternoon on July 19 by carefully removing a 50 cm wide ring of bark approximately 2 m above the ground (approximately 0.6 m above the sap flow probes) using a sharp knife and draw blade. The bark peeled easily at the cambium allowing us to avoid injury to the xylem. At the end of the study, we verified the presence (beetle infested trees) or absence (control and girdled trees) of blue stain fungi in sapwood tissue of each treatment by extracting an increment core from each tree and by visually examining the xylem tissue below a 2 cm square section of bark. Blue stain fungal mycelium was present in the sapwood of all beetle infested trees and was absent in cores from the girdled and control trees.

2.3. Environmental data

Environmental variables were measured using the long term meteorological station at Fraser Experimental Forest located within 50 m of our study site and were used to quantify transpiration driving variables and light saturated canopy conductance. We measured air temperature and relative humidity (HMP45C, Campbell Scientific, Logan Utah, USA), wind speed and direction at 10 m (5103 wind monitor, RM Young CO., Traverse City MI, USA), and photosynthetically active radiation above the forest canopy (LI-190, LICOR, Inc., Lincoln, NB, USA). Sensors were connected to a Campbell Scientific 23× data logger, measured every ten seconds, averaged and recorded on ten minute intervals.

2.4. Sap flux density and canopy conductance measurements

Sap flux density (v , $\text{g cm}^{-2} \text{ s}^{-1}$) was determined using a single Granier style heat dissipation probes (Granier, 1987) for each measurement tree. Probes were installed on the north side of each tree (to prevent solar heating) at approximately 1.4 m above ground level. We estimated sapwood area (SWA) for treatment trees as a linear function of diameter at breast height (DBH) using data from previous studies at FEF, ((Ryan, 1989; Kaufmann, 1995) $\text{SWA} = \text{DBH} \times 11.17 - 46.9$, $R^2 = 0.70$). Estimates of sapwood thickness indicated that probe lengths measured sap flux density over at least 70% of the sapwood thickness for all trees. Probes were insulated from thermal gradients using a closed cell foam block and foil backed insulation reflecting 96% of incoming radiant energy (Reflectix Inc., Markleville, IN) and were protected from moisture and stem flow using plastic sheeting. Sap flow probes were connected to a data logger equipped with a multiplexer (CR10x and AM16/32, Campbell Scientific Inc., Logan, UT) and 10 s instantaneous v measurements were averaged, recorded every 10 min

and used to obtain daily estimates of v . Sap flux density measurements began approximately 10 days before treatments began and continued through August 2006 when we were forced to cease measurements due to equipment malfunction. In 2007, we measured v from early April until the end of September.

Canopy transpiration (E_c) for each tree was calculated as the product of v and SWA. Transpiration per unit leaf area (E_l) for each tree was calculated in a similar way as the quotient of E_c and total projected leaf area (LA); calculated from allometric relationships derived at FEF for lodgepole pine (Kaufmann et al., 1982). We estimated canopy conductance (G_t , $\text{mmol m}^{-2} \text{ leaf area s}^{-1}$) under light saturated conditions for lodgepole pine photosynthesis (Schoettle and Smith, 1999) as:

$$G_t = E_l/D \quad (1)$$

where D is air saturation deficit in partial pressure units (kPa/kPa) (Whitehead et al., 1996).

Because measurement trees were located in a relatively open stand, we assumed the canopy was tightly coupled to the atmosphere and verified this assumption based on an analysis of changes in sap flux density with wind speed (Hubbard et al., 2004). Differences between treatments were assessed by averaging G_t for the 2007 growing season by 0.25 kPa D classes.

2.5. Leaf water potential and foliar expansion measurements

Pre-dawn leaf water potential (Ψ_{leaf}) was measured every seven to ten days following beetle infestation in 2006 and measurements were continued throughout the second growing season (2007). Three trees from each treatment were randomly selected the day before measurements. Prior to sunrise on the day of measurement, we removed a small branch using a pole pruner from a randomly selected location in the middle third of the canopy. Predawn leaf water potential was measured on three fully expanded needles immediately following branch cutting using a Scholander type pressure chamber (PMS Instruments, Albany, OR, USA). Once Ψ_{leaf} was less than -6 MPa, the measurement was stopped because -6 MPa is well beyond the point of catastrophic xylem failure in lodgepole pine (Tyree and Sperry, 1988; Pinol and Sala, 2000).

We measured the rate of needle expansion for the 2007 foliage on the same branches that were removed for Ψ_{leaf} measurements ($n = 3$). Because we could not follow the expansion of individual needles due to lack of canopy access, we measured the lengths of new, expanding needles relative to the length of the prior year's foliage for each treatment and calculated needle expansion as the percentage of the two.

2.6. Statistical analysis

The individual tree was the sampling unit for all analyses. After verifying assumptions of normality and homogeneity of variance, we utilized a piecewise regression approach (Neter et al., 1990) to determine the exact timing of changes in canopy transpiration following beetle infestation and phloem girdling treatments in 2006. We calculated the mean daily ratio of E_c between the control and treatment trees and fit two separate linear regression equations to the data before and after beetle attack and girdle treatments respectively. We determined the date where these two equations were equal to quantify the point at which treatments began affecting transpiration and calculated bootstrapped confidence intervals to estimate the error around the date of change. Differences in pre-dawn leaf water potentials were assessed using the GLIMMIX procedure in SAS (version 9.2; SAS Institute, Cary, NC, USA) with a spatial exponential residual covariance structure to ac-

count for uneven sample periods. GLIMMIX was also used to quantify treatment differences in mean sap flux density between treatments in 2007 as well as the treatment response of G_t with D using a first-order autoregressive residual covariance structure. We quantified differences in foliar expansion rates between treatments using One-Way analysis of variance (SPSS, Inc., New York, NY, USA).

3. Results

Bark beetles infested trees in our experimental site on June 19, 2006. Within ten days (± 4 days) canopy transpiration began to decline relative to control trees. By the end of August, 2006, average transpiration in beetle attacked trees was 60% lower than control trees (Fig. 1). Differences in mean pre-dawn leaf water potentials were not apparent between the control and beetle attacked trees until later in the summer when water potentials were significantly more negative (Fig. 1, $p < 0.01$). Although E_c also declined after installation of the girdle treatment, pre-dawn leaf water potential did not differ between girdle and control treatments (Fig. 1, $p = 0.95$).

At the beginning of the second growing season (2007), sap flux density for the beetle attacked treatment declined quickly to zero and was significantly different than control and girdled treatments ($p < 0.01$, Fig. 2). Mean weekly v gradually increased in control trees, peaking near the middle of June then gradually declined until October. Mean sap flux density in the girdle treatment followed the same general pattern as controls but was generally lower except for four weeks in late May and early June ($p > 0.1$, Fig. 2). Pre-dawn leaf water potentials were similar between control and girdle treatments throughout the second growing season (2007) while water potential in beetle attacked trees declined quickly in the spring to < -6.0 MPa and did not recover (Fig. 3).

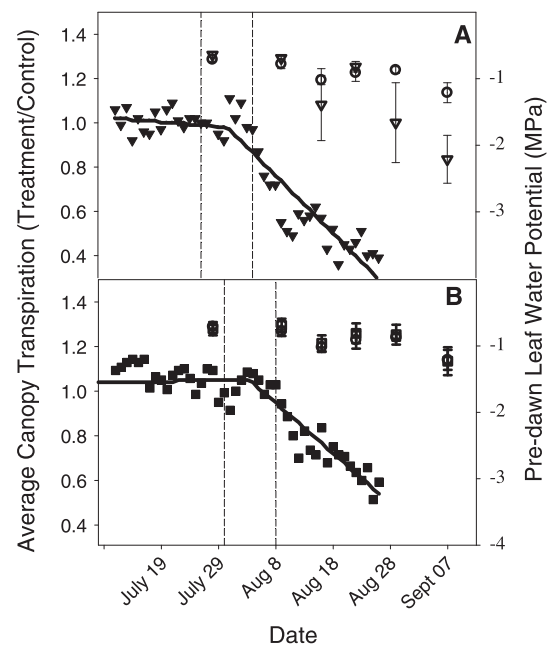


Fig. 1. Ratio of average canopy transpiration rates of beetle attacked (A) and girdled (B) trees to the average canopy transpiration rate of control trees (left axis) and pre-dawn leaf water potential (right axis) in 2006. Dashed lines indicate 95% bootstrapped confidence intervals of the date transpiration rates of the two treatments began to significantly differ from controls. Treatments (bark beetle attack and girdling) began on DOY 200. Error bars for pre-dawn water potential measurements represent standard error of the mean for three trees per sampling period.

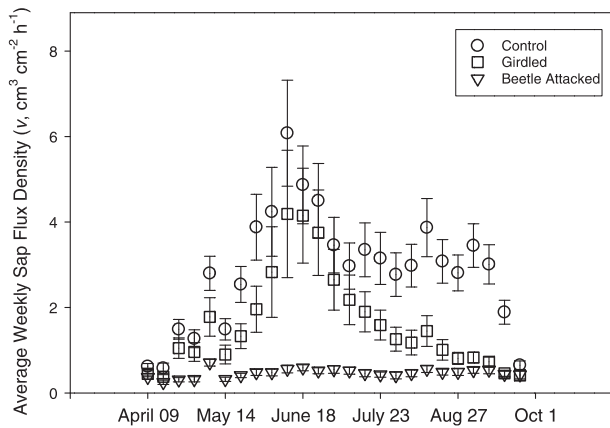


Fig. 2. Average sapflux density of beetle attacked (▽), girdled (□) and control (○) trees during 2007. Errors bars represent the standard error of the mean.

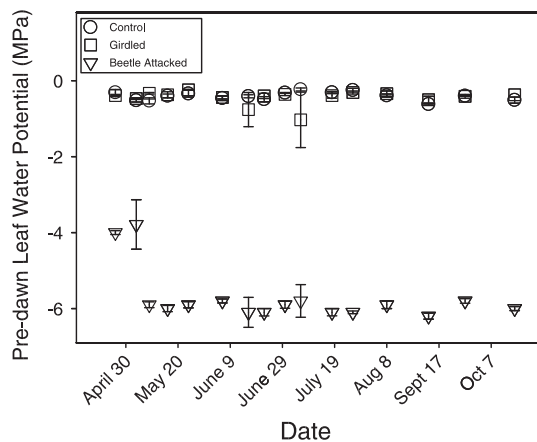


Fig. 3. Pre-dawn leaf water potential of beetle attacked (▽), girdled (□) and control (○) trees during 2007. Errors bars represent the standard error of the mean.

During the second growing season (2007), light saturated canopy conductance exhibited a typical decline with increasing saturation vapor pressure deficit for the control and girdled treatment while canopy conductance for beetle attacked trees remained close to zero even at low D . Differences between control and girdled trees were significant below D values of 2.0 kPa ($p < 0.05$, Fig. 5). Although G_t was slightly higher for control trees across all D values, differences were not significant when D was greater than 2.0 kPa.

The expansion rate of new foliage did not differ between trees for the control and girdle treatments respectively ($p = 0.15$). Buds containing 2007 foliage on the beetle attacked trees failed to open at the beginning of the season and did not grow during 2007. New needle growth on control and girdle treatments began in early June and was complete by early August (Fig. 4).

4. Discussion

The rapid decline in transpiration of beetle attacked trees in this study was consistent with our prediction that fungal infection from bark beetles causes drought related tree mortality. In spite of no visible signs of needle discoloration, transpiration in beetle attacked trees declined nearly 60% relative to controls by the end of the first growing season (2006). Yamaoka et al. (1990) found a similar rapid decline in transpiration ten to 13 days after inoculating lodgepole pine trees with the blue-stain fungi *Ophiostoma montium*. Miller

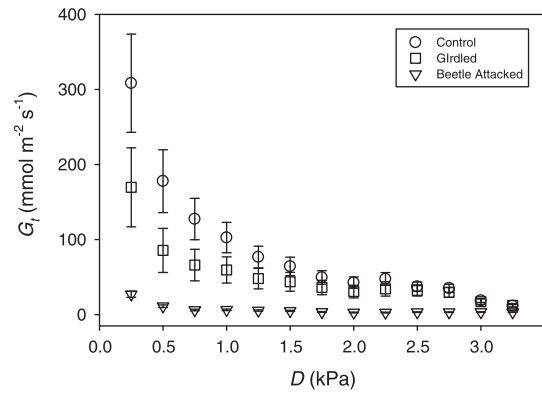


Fig. 4. Canopy conductance (G_t) versus air saturation deficit during 2007 for beetle attacked (▽), girdled (□) and control (○) trees during 2007. Errors bars represent the standard error of the mean.

et al. (1986) found a reduction in sap velocity approximately ten days following beetle attack in a single *Pinus contorta* tree and Wullschlegel et al. (2004) reported a significant decline in transpiration in *Pinus taeda* trees following attack by the southern pine beetle (*Dendroctonus frontalis* Zimm.) however changes were not apparent until later in the summer. Although transpiration also declined in girdled treatments relative to control trees soon after beetle attack, pre-dawn water potential measurements did not differ between treatments throughout both growing seasons suggesting that girdled trees did not experience any additional water limitation. The decline in transpiration in girdled treatments was possibly a wound response or a decline in stomatal conductance due to decreased demand for photosynthate from root tissues.

Differences in canopy transpiration between girdled and control trees were not consistent during the second growing season (2007), probably because of changes in carbon sinks as new 2007 foliage expanded during June and July. Girdled trees in this study experienced a significant change in their source sink relationships as the girdle treatment completely cut off photosynthate transport to stem and root tissues below the girdled portion of the stem. Other studies in conifers have shown that new foliage depends on carbon from older foliage until the new foliage is photosynthetically capable of being autotrophic (Chung and Barnes, 1980; Kozłowski, 1992; Radoglou and Teskey, 1997). Similarly, spring girdling of loblolly pine stems immediately halted growth below the girdle and increased growth above the girdle, suggesting that current photosynthate controlled early stem growth (Maier et al.

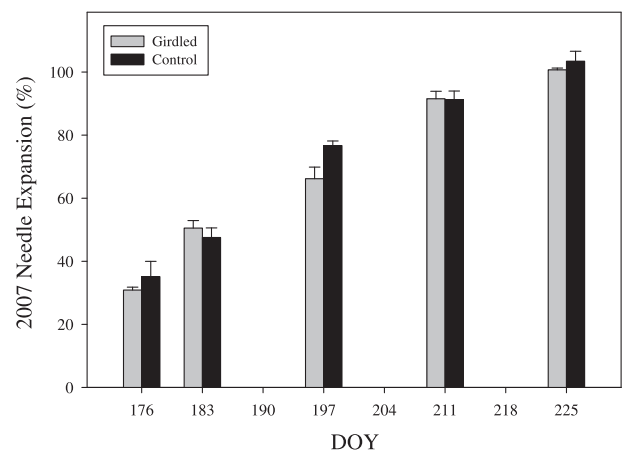


Fig. 5. 2007 Needle expansion for control (open bars) and girdled (solid bars) treatments. Foliage on beetle attacked trees did not grow during 2007. Errors bars represent the standard error of the mean.

2010). Although circumstantial, our data suggests that most of the carbon for foliar expansion in this study is likely from newly formed photosynthate in older foliage since expansion of foliage coincided with increased sap flux density and canopy conductance.

Blue stain fungi rather than phloem feeding appears to be the primary cause of mortality in the beetle-attacked lodgepole pine. Trees that were completely girdled continued to grow during the growing season following treatment whereas the beetle-attacked trees did not. Beetles likely consume much less phloem than the 100% girdling treatment; in a complementary survey we estimated that bark beetles damaged ~45% of the phloem surface area ($n = 38$ trees). As such, beetle activity would not inhibit photosynthate transport to the extent as our girdling treatment. However it is possible that results could differ for other species of bark beetles because not all species consume phloem at the same rate depending on species specific nutrient acquisition strategies (Ayres et al., 2000). In addition, potential fungal growth in to phloem tissue may also inhibit photosynthate transport and would exacerbate effects due to phloem consumption by beetles and their larvae.

Although our results suggest that fungal infection of the sapwood caused tree mortality in the bark beetle infested trees we studied, our data do not necessarily imply that fungi play an important role in the establishment of bark beetles on living conifers. In addition, it is possible that there was some degree of secondary fungal infection following beetle attack that influenced our results. There are conflicting views in the literature as to the role fungi play in overwhelming tree defenses and several detailed reviews explore the pros and cons of evidence relating to bark beetle and fungi commensalisms (Paine et al., 1997; Lieutier et al., 2009; Six and Wingfield, 2011). The extent that blue-stain fungi conferred an increased ability of bark beetles to overwhelm tree defenses was not measured in this study and we did not collect data on beetle/fungal associations for the bark beetles that attacked our treatment trees. However, our results clearly show that fungi associated with *Dendroctonus ponderosae* are strongly involved in causing tree mortality by reducing the flow of water from the soil to the canopy rather than any girdling effects by beetles.

Susceptibility of lodgepole pine to attack by mountain pine beetle has been shown to be directly related to tree vigor (growth per unit leaf area) because an increased tree growth rate may facilitate a tree's ability to allocate more resources to defense compounds (Mitchell et al., 1983; Waring and Pitman, 1985; Christiansen et al., 1987; Coops et al., 2009). We could not directly test the relationship between tree vigor and bark beetle attack in this study because we randomly selected two thirds of the trees and sprayed them with insecticide to prevent attack and because stem growth rates were not measured. However, uninfested trees had a slightly higher ratio of sapwood area to leaf area ($p = 0.049$, calculated from allometric relationships (Kaufmann et al., 1982)) suggesting that the trees not attacked by MPB may have had a higher physiological vigor than those succumbing to bark beetles. The degree to which this altered resistance to bark beetle attack in this study is uncertain.

4.1. Implications

Rapid changes in transpiration following beetle attack will likely influence site water balance in subalpine watersheds experiencing large scale bark beetle infestations. Our data suggest there will be an increase in soil water availability throughout the first growing season following mountain pine beetle attack and increased water availability resulting from dead trees will reach a maximum as early as the second growing season. Increased water availability could potentially improve plant water status of trees and species unaffected by mountain pine beetle or provide increased runoff to streamflow. The magnitude of these changes will depend on the

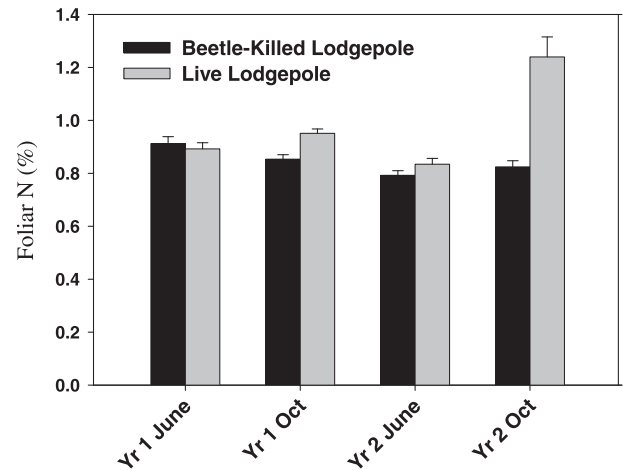


Fig. 6. Nitrogen concentration pine needles on beetle attacked ($n = 17$ trees) and live control trees ($n = 10$ trees). Needles were collected from 2005 and 2006 needle cohorts located in the external portion of mid-canopy branches during June and October of 2006 (Yr 1) and 2007 (Yr 2). Nitrogen was analyzed by LECO dry combustion. The foliar N content of live trees was higher than all previous dates ($p < 0.01$). Errors bars represent the standard error of the mean.

severity of MPB infestation, stand structure and climate and are currently being studied at several locations within FEF.

Other ecosystem processes will respond to extensive overstory mortality and reduced water use as overstory pine trees succumb to bark beetles. Demand for plant nutrients, such as the nitrate form of nitrogen that are passively absorbed within the transpiration stream, will drop off with declining water use. For example, two independent studies in Colorado lodgepole forests found that soil moisture and plant available soil nitrogen, including nitrate were higher beneath the canopies of individual red and grey phase trees, as opposed to adjacent green lodgepole pine (Clow et al., 2011; Xiong et al., 2011). In the current study, the foliar N content of surviving overstory trees increased as the majority of trees in the stand succumbed to bark beetles (Fig 6). Understory trees are also growing faster as canopy mortality progresses in lodgepole pine stands at the Fraser Experimental Forest (Collins et al., 2011). Compensatory growth as vegetation responds to declining water and nutrient use by overstory pines will influence the magnitude and timing of watershed-scale consequences of the bark beetle outbreak.

Widespread tree mortality resulting from MPB infestations throughout western North America has raised concerns regarding potential increased fire risk in beetle killed stands (Jenkins et al., 2008). Little is known about how MPB infestations influence fire behavior but recent studies suggest there are significant differences between fire in live versus beetle killed forests (Klutsch et al., 2009; Cruz and Alexander, 2010; Simard et al., 2011; Collins et al., in preparation). A recent study by Jolly et al. (2012) found lower foliar moisture and increased flammability in foliage from recently attacked trees suggesting that fire risk immediately following MPB infestation may increase while the foliage remains on the trees. Current models of fire behavior in beetle killed forests will need to be modified to account for rapidly changing foliar moisture dynamics soon after beetle attack (Cruz and Alexander, 2010; Jolly et al., 2012). The rapid decline in transpiration rates and leaf water potential in beetle attacked trees in this study supports the idea that changes in foliar moisture will have important implications for fire risk and behavior within weeks of bark beetle infestation.

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