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Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack

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ABSTRACT

Very little is known about how foliar moisture and chemistry change after a mountain pine beetle attack and even less is known about how these intrinsic foliar characteristics alter foliage ignitability. Here, we examine the fuel characteristics and ignition potential of *Pinus contorta* (lodgepole pine) foliage during the early stages of a mountain pine beetle attack. Foliar samples were taken periodically from multiple trees identified as green (healthy, unattacked), recently attacked, or red (dead). The fuel moisture content, chemical composition, and time to ignition of needles from each attack category were quantified. Foliar moisture contents varied by an order of magnitude between the attack categories and were lowest for red needles (~12% on average), highest for green needles (~109% on average), and most variable for needles of recently attacked trees. Dry matter proportions of fiber in the needles of attacked and red trees were nearly twice that of green needles. Starch and sugar levels were much lower in the needles of attacked and red trees than green trees. Crude fat contents also differed between the attack categories. Time to ignition was strongly related to time since beetle attack. Ignition times varied from as little as 11 s for red needles to 41 s for green needles. A combined model of foliar moisture content, fiber, and crude fat explained 92% of the variation in the foliar time to ignition. Results show that decreased moisture contents and changes in foliar chemistry increase the foliar flammability of mountain pine beetle-attacked trees. This suggests that less heat would be required to ignite the foliage of attacked trees and thus crown fire potential may be higher in attacked stands as long as foliage is retained on the tree.

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1. Introduction

Mountain pine beetles (*Dendroctonus ponderosae*) (MPB) are native insects that play an important role in the natural disturbance cycle in western North American forests (Sartwell and Stevens, 1975). These beetles attack a variety of host tree species including lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), and other pines (Veblen et al., 1989). Although endemic MPB populations are always present, epidemic outbreaks that sweep across large areas, kill many trees, and alter forest structure are periodic (Berryman, 1982; Waring and Pitman, 1985). A large-scale outbreak is currently underway in the forests of western North America. Over 3.4 million hectares of US forests have been killed by MPB (US Forest Service, 2009), and over 13 million hectares of Canadian forests have been killed by MPB (Kurz et al., 2008). A recent study reported the first successful overwintering of MPB in jack pine (*Pinus banksiana*) which could increase the range of MPB and result in even more widespread attacks across North America by making the boreal region susceptible (Cullingham et al., 2011).

Early during a MPB attack, trees undergo rapid physiological changes as the beetles and their larvae consume phloem tissue and inoculate the xylem with blue stain fungi (*Ophiostoma* spp.). Changes in stem moisture content can be observed as early as 2 weeks after a successful attack (Yamaoka et al., 1990), and stem moisture drops an order of magnitude during the first year of an attack (Reid, 1961). Foliage color may change from green to yellow by the end of the first year as the needles desiccate and from yellow to red in the following year (Wulder et al., 2006).

In MPB-attacked stands, numerous visual and structural changes occur over time, but understanding how these observable changes relate to chemical and fuel changes requires field measurements and empirical study. Foliage color changes may be associated with changes in moisture content and chemical composition, and needle loss and weakened stems will alter surface and canopy fuel profiles. Large changes in foliar moisture content (FMC) as a result of other pathogen attacks have been reported (Kuljian and Varner, 2010), but these changes have not been quantified for MPB-attacked trees.

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Following an attack, tree crown structure and vertical biomass distributions begin to change dramatically. After about 2 or 3 years, red needles abscise and fall to the forest floor (British Columbia Ministry of Forests, 1995; Jae-Jin Kim et al., 2005). After about 10 years, dead aerial stems fall to the ground (Page and Jenkins, 2007a; Simard et al., 2011), and as surface light availability increases, understory biomass can increase by an order of magnitude, adding to already increasing surface fuels (Stone and Wolfe, 1996).

Changes in fuel characteristics and distributions may alter the spread and intensity of wildfires in attacked stands (Page and Jenkins, 2007b; Jenkins et al., 2008) but the magnitude and type of change is uncertain. In the absence of any structural changes within a tree's crown, such as needle loss, the strong relationship between conifer foliar moisture and foliar ignitability suggests that foliage desiccation may increase crown flammability (Xanthopoulos and Wakimoto, 1993). However, as needles fall, crown foliar biomass is reduced, which may reduce the likelihood of crown ignition in attacked stands (Van Wagner, 1977), but as needle litter amounts increase, so may surface fire intensity. An increase in the likelihood of passive crown fire, where only small groups of overstory trees ignite, instead of active crown fire, where fires spread from tree crown to tree crown, is also possible (Klutsch et al., 2011). As stems fall in beetle-killed stands, there can be as much as a fourfold increase in the coarse woody debris on the forest floor (Klutsch et al., 2009), and surface fire intensities can be higher for years after an attack (Page and Jenkins, 2007b).

Some researchers have attempted to model wildland fire behavior in MPB-altered fuel structures using the simple fire behavior prediction models developed by Rothermel (1972) and Van Wagner (1977). These models are implemented in fire behavior modeling systems such as BehavePlus (Andrews et al., 2008), NEXUS (Scott, 1999; Scott and Reinhardt, 2001) and FARSITE (Finney, 2004). Page and Jenkins (2007b) used field data to develop custom fuel models to drive fire behavior models to estimate expected changes in surface fire intensity and spread rate in MPB-attacked stands. Page and Jenkins (2007b) understood that their model could only reliably predict the conditions necessary for transition from a surface fire to a crown fire in stands with foliar moisture contents greater than ~70% (Van Wagner, 1977; Page and Jenkins, 2007b; Jenkins et al., 2008). Simard et al. (2011) suggested that actively spreading crown fires were less likely under moderate weather conditions after an outbreak, but the Van Wagner crown fire model that they used may not be valid for addressing this question because it cannot deal with the inherent variations in fuel moisture and heterogeneity that develop after a beetle attack (Jolly et al., in press). Klutsch et al. (2011) used custom fuel models in the Fire and Fuels Extension of the Forest Vegetation Simulator to model potential crown fire behavior by removing needles of MPB-infested trees from canopy fuel loads. They determined that the species composition of surviving trees was an important factor in crown fire behavior and that in both infested and uninfested stands the probability of crown fire was high resulting in very high fire-caused mortality of remaining trees. Essentially, there is a near void of empirical evidence relating fuel characteristics and foliage flammability across a range of MPB attack conditions, and nearly all studies have been forced to use unverified models to address these problems.

The fire behavior modeling systems currently used in wildland fire operations and management in the United States may fail to adequately assess fire behavior changes in beetle-attacked stands, even though these tools are the only ones available for operational fire behavior assessments (Cruz and Alexander, 2010). While the presence of dead foliage may increase the likelihood of transitioning from surface to crown fire, fine-scale heterogeneity, which is typical in attacked stands, is likely to influence the likelihood of fire reaching tree crowns. Because stand-scale models consider a stand as having a single averaged set of conditions, they cannot accommodate the significant fine-scale fuel moisture heterogeneity that exists between adjacent attacked and undisturbed trees. More recently developed three-dimensional, computational fluid dynamics-based fire behavior fuel models, such as the *Wildland Fire Dynamics Simulator* (WFDS) (Mell et al., 2009) or *FIRETEC* (Linn et al., 2002, 2005), which are sensitive to spatial heterogeneity in fuels and model the physical processes of combustion and heat transfer in detail, may improve our ability to model fire behavior in beetle-attacked stands. However, fuel characteristics needed to simulate fire behavior in beetle-attacked stands, such as foliar moisture content, have not been reported in the available literature. Regardless of the fire behavior modeling system utilized, incorporating field measurements collected from fuels across the range of conditions in MPB-attacked stands is necessary to improve fire behavior simulations.

Here, we present the results of a study aimed at quantifying the influence of fuel moisture and foliar chemistry on the ignitability of lodgepole pine needles during the early stages of an MPB attack. We measured the moisture content and chemical composition of foliage throughout the growing season, and we ignited foliar samples in a controlled laboratory environment to determine the flammability of foliage during early stages of a MPB attack. Our objectives were to contribute key fuels information to fire behavior models and better understand how foliage flammability changes during the early stages of a MPB attack and how an attack will influence the likelihood of passive or active crown fire.

2. Materials and methods

2.1. Study sites selection

Foliar samples were taken over time in two stands in north-central Colorado and one stand in western Montana. The first Colorado site was located in the Fraser Experimental Forest at an elevation of ~2678 (8789 ft) (39.9277° Lat., −105.8223° Long.) and was dominated by lodgepole pine with scattered Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The second Colorado site was a pure lodgepole pine stand near Cameron Pass in the Arapaho-Roosevelt National Forest at an elevation of ~2658 m (8700 ft) (40.6173° Lat., −05.8194° Long). The Montana site was located on the Lolo National Forest in western Montana at an elevation of about ~2031 m (6666 ft) (hereafter referred to as Point 6) (47.01367° Lat., −114.0143° Long.) and was also a nearly-pure lodgepole pine stand with a small percentage of subalpine fir. Foliar moisture content variations were measured at both the Colorado and Montana sites and foliar chemistry and time to ignition were determined for foliage samples collected from the Montana Point 6 site.

2.2. Characteristics of trees in MPB-attacked stands

Trees were stratified into three categories: green (unattacked), successfully attacked (dying), and red (dead) trees. Where possible, successfully attacked trees were classified as either being attacked the previous year or the current year. Trees attacked the previous year had started to show leaf discoloration and their needles were yellow or orange while trees attacked during the current year still had green foliage. These categories were easily identified in the field using visual indicators of needle discoloration and the presence of pitch tubes and other signs of attack and thus could be used to facilitate assessments of the potential differences in burning characteristics between categories. Green trees were those with lush green foliage and no obvious signs of MPB attack. Attacked trees were those with abundant pitch tubes and boring dust

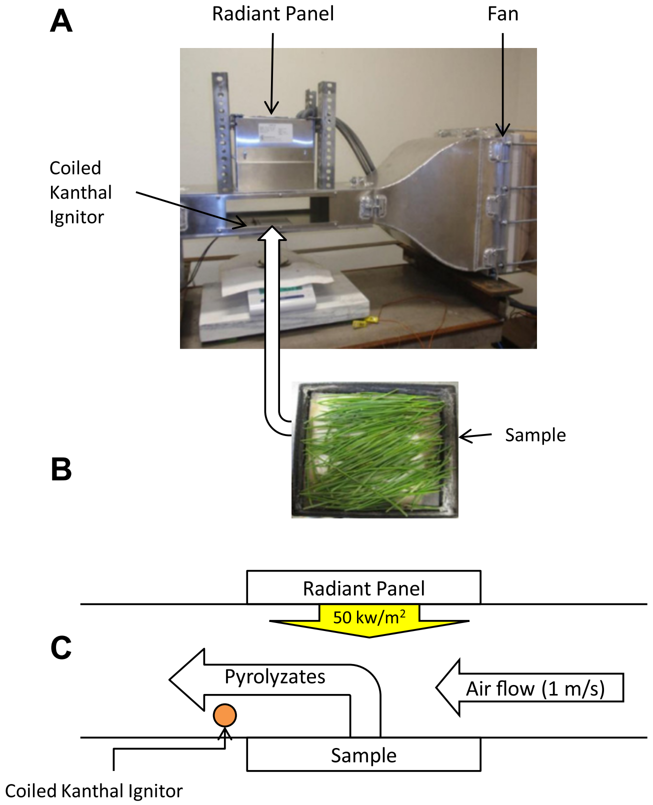

Fig. 1. Forced Ignition and Flame Spread (FIST) ignition apparatus used to measure the time to ignition of foliar samples in the laboratory. (A) Ignition apparatus: small-scale wind tunnel with infrared panel and piloted ignition source. (B) Sample: an example green lodgepole pine sample prior to ignition. (C) Schematic of experimental set-up detailing air flow within the apparatus. Samples are heated from above by the radiant panel and the pyrolyzates produced from the heated sample are carried over the Kanthal ignitor by a fixed air flow. When sufficient pyrolyzates are produced, ignition occurs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

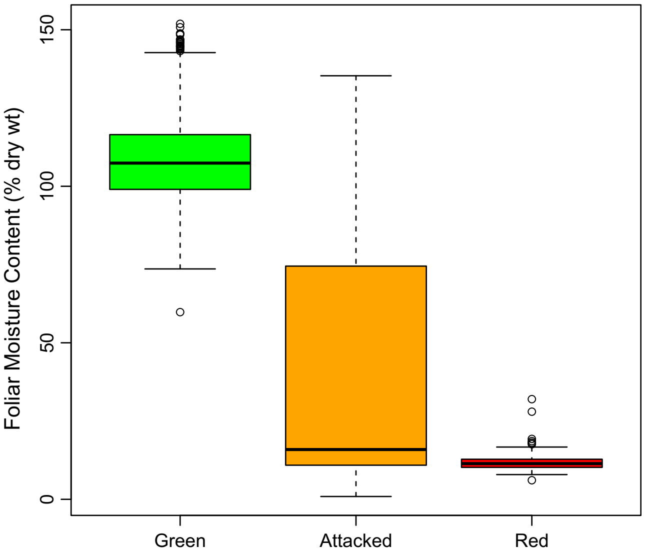

Fig. 2. Box plot of growing season variations in lodgepole pine foliar moisture contents during the early stages of MPB attack. Boxes represent the interquartile range and horizontal lines within the boxes indicate the medians for each category. Upper and lower whiskers are displayed as 1.5 times the interquartile (1.5 IQR). Open circles are observed values that fall outside of the 1.5 IQR ranges.

(Amman et al., 1990) and their needles were either still green or were just turning yellow or orange at the time they were identified. Red (dead) trees were those with 100% red foliage.

2.3. Foliar moisture content

Foliar samples were collected from the two sites in Colorado and samples were taken from 12 successfully attacked and 12 green overstory lodgepole pine trees in both stands. Successfully attacked trees were killed by MPB the summer before sampling and green trees were undisturbed at the start of the study. All trees in each stand were part of the same cohort. Sampling in the Fraser Experimental Forest stand began May 2007 and continued weekly through the end of September 2007. In 2008, sampling occurred at about 3-week intervals until 17 June 2008, when samples were collected every 2 weeks through 9 September 2008. In August 2007, four newly attacked trees and five more green trees were added for sampling. Sampling in the Cameron Pass stand began in June of 2009 and continued nearly biweekly through late September 2009. In 2010, foliar moisture samples were collected about once a month until the beginning of April 2010 when samples were collected every 2–3 weeks through the middle of August 2010. Three previously unattacked trees were attacked by mountain pine beetle during the summer of 2009 and were subsequently added to the attacked category. Foliage samples from both Colorado sites were collected from the lower third of the crown on the south side of each tree and included all needles from the branch tip to the oldest foliage. One, ~4 g foliar sample was collected from each tree at each site early in the morning, placed in plastic bags, stored in a cooler, and transported to the laboratory for immediate processing. Woody material including fascicles was removed. Needles were weighed, dried for at least 3 days in a forced-convection oven at 60 °C (140 F) and reweighed.

At the Point 6 site in Montana, seven trees were randomly selected from the green and red categories, and 14 trees were selected from the attacked category ($n_{\text{trees}} = 28$). The site had been attacked by MPB within the last 2 years, but the stand included green, recently attacked, and dead (red) trees. Sampling began in June 2010 and continued weekly through the end of the snow-free period in October 2010. Trees were tagged with sequentially numbered, aluminum tags so that the same trees were tracked throughout the season. Foliar samples were collected from the lower third of the tree crown. Three foliage samples, weighing ~2 g each, were collected from each tree, weighed to the nearest 10 mg, dried for at least 2 days in a in a forced-convection oven at 95 °C (203 F), and reweighed. Foliar moisture content for all sites were expressed as a percentage of dry weight (Norum and Miller, 1984). Slightly different drying temperatures were used at the Colorado and Montana sites but comparisons of the same needle samples dried at both temperatures were nearly identical and thus these two datasets were combined for our analysis.

2.4. Chemical composition analysis

Each week, a 20 g sample was collected from one green tree, one red tree, and two attacked trees for foliar chemistry. To minimize between tree variability, samples were taken from the same green, attacked, and red trees throughout the season. The chemical composition of needles was determined using the wet reference method by an external forage testing laboratory (Association of Official Agricultural Chemists, 2005; AgriAnalysis, 2011). The foliar chemical analysis provided dry weights percentages of crude protein (CP), crude fat (CF), neutral detergent fiber (NDF), ash content (AC), and non-fiber carbohydrates (NFC). Crude protein was determined using a TruSpec combustion analyzer. Crude fat was determined using an ANKOM Analyzer with petroleum ether.

Table 1
Growing season minimum, maximum, mean and standard deviations of lodgepole pine foliar moisture contents (FMC) in the early stages following a MPB attack. Mean FMC values were significantly different between groups ($p < 0.001$; $F = 2487.2$, $n = 2642$).

Tree condition	Minimum FMC (% dry weight)	Maximum FMC (% dry weight)	Mean and standard deviation FMC (% dry weight)
Green	40.0	120.3	108.5 (14.1)
Attacked	0.9	125.2	38.57 (37.4)
Red	6.1	32.0	11.7 (2.6)

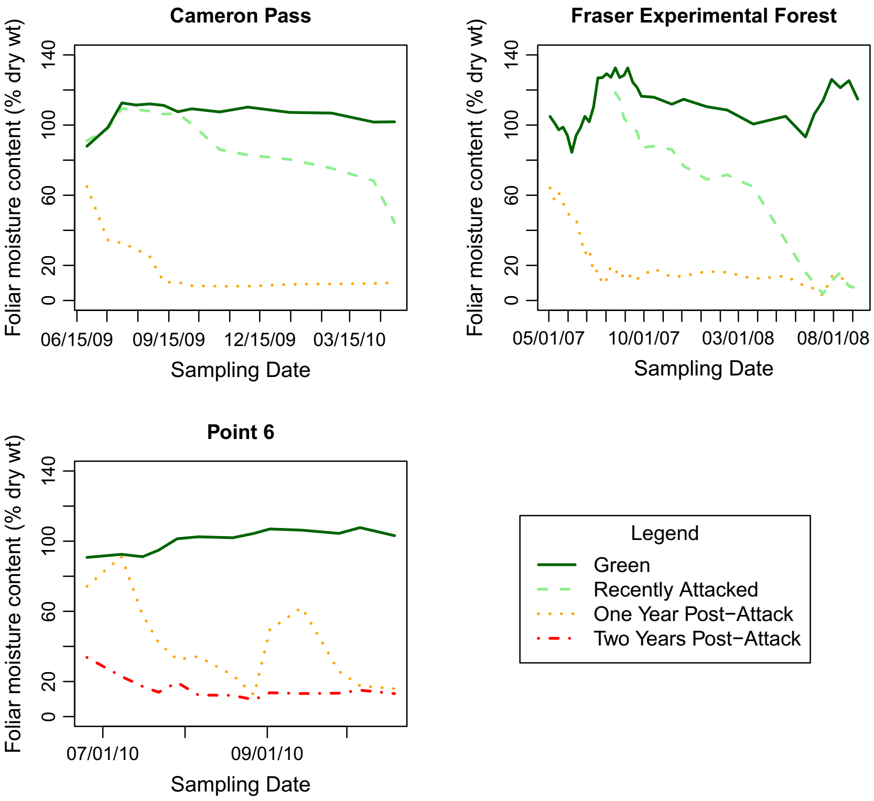

Fig. 3. Lodgepole pine foliar moisture content time series for the early stages following a MPB attack at three sites. Line colors and types indicate the condition of trees when sampling began. Solid lines (dark green) were green, unattacked trees, dashed lines (light green) were recently attacked (<1 year, since MPB attack), dotted lines (yellow) had been attacked for 1 year, and dashed-dotted lines (red) had been attacked for 2 years. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Mean and standard deviations of growing-season dry matter allocation of lodgepole pine foliage in five chemical categories across a range of conditions observed in the first stages following a MPB attack. The means of all foliar chemistry components varied significantly between groups.

Tree condition	Fiber carbohydrates*** (% dry matter)	Non-fiber carbohydrates*** (% dry matter)	Fat*** (% dry matter)	Ash* (% dry matter)	Protein*** (% dry matter)
Green	39.6 (2.1)	43.4 (2.2)	7.1 (0.4)	2.5 (0.1)	7.5 (0.7)
Attacked	59.7 (9.6)	25.6 (9.1)	4.5 (0.9)	2.7 (0.3)	7.5 (0.6)
Red	65.2 (1.6)	20.1 (2.0)	5.7 (0.7)	2.5 (0.3)	6.5 (0.7)

NS = not significant.
[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

Neutral detergent fiber was determined using an ANKOM 200 Fiber Analyzer. Ash content was determined by completely combusting a foliage sample in a muffle furnace and weighing the remaining residue. Non-fiber carbohydrate percentages were determined using the difference method and the following equation:

$$\mathrm{NFC} = 100 - (\mathrm{NDF} + \mathrm{CF} + \mathrm{CP} + \mathrm{AC})$$

Neutral detergent fiber levels identify the structural carbohydrates such as cellulose, hemicellulose, and lignin present in needles. Non-fiber carbohydrate levels identify the water soluble carbohydrates, such as sugars, starches, and other non-structural carbon compounds present in needles. Crude protein is generally proportional to the amount of nitrogen in each sample. Crude fats quantify the amount of isoprenoids, waxes, and oils present in the

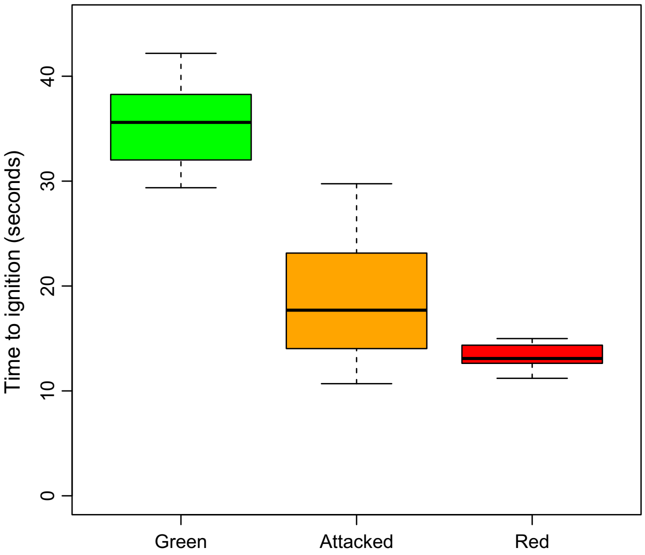

Fig. 4. Box plot of ranges of time to ignition of lodgepole pine foliage across three early stages following a MPB attack. Boxes represent the interquartile range and horizontal lines within the boxes indicate the medians for each category. Upper and lower whiskers are displayed as 1.5 times the interquartile (1.5 IQR). Open circles are observed values that fall outside of the 1.5 IQR ranges.

Table 3
Growing season averages and extremes of the time to ignition for lodgepole pine foliage across the early stages of a MPB attack. Mean time to ignition varied significantly between attack categories (ANOVA, $p < 0.001$, $F = 91.268$, $n = 48$).

Tree condition	Seasonal minimum time to ignition (s)	Seasonal maximum time to ignition (s)	Seasonal mean and standard deviation of time to ignition (s)
Green	29.4	42.2	35.3 (4.1)
Attacked	10.7	29.8	18.7 (5.1)
Red	11.2	15.0	13.3 (1.2)

foliage, and ash content is related to the percentage of foliage made up of minerals or inorganic compounds (Kozlowski and Pallardy, 1979).

2.5. Time to ignition measurements

Time to ignition was measured each week on samples taken from one green, two attacked, and one red tree at the Montana site. We ignited three, 4 g samples from each of the four trees sampled using an apparatus that was built to measure the ignition time for sustained flaming ignition of woody. It consists of a small-scale wind tunnel, an infrared heater, and a coiled wire igniter and operates according to the Forced Ignition and Flame Spread Test (Cordova et al., 2001) (Fig. 1A). The wind tunnel measures 9 cm tall, 25 cm wide, and 60 cm long. Its fan produces a laminar forced airflow through the tunnel with a velocity of 0.8–1.6 m/s, which corresponds to Reynold's numbers of 3–6.104, well less than the transition to turbulent flow. Foliar samples are held in a thin, lightweight aluminum box (9 × 9 × 2.5 cm) lined with Cotronics-brand ceramic paper and a 1.27 cm thick Cotronics-brand ceramic board on the bottom (Fig. 1B). The sample holder is mounted with the upper surface of the sample flush with the bottom of the tunnel. The sample is heated from above using an infrared heater capable of producing a uniform heat flux up to 50 kW/m^2 over the sample surface. As the sample is heated, pyrolysis begins, and the forced flow pushes the pyrolysis gases into the coiled Kanthal wire igniter where the gases are ignited. To exclude igniter location as a potential variable in the experiments, the 3.5-mm diameter igniter was fixed at a position that covered the entire fuel concentration boundary layer and the supplied current was calibrated to keep the igniter above 1000 °C. Time to ignition (t_{ig}) was recorded as the time from the initiation of heating to the time at which a flame was sustained over the surface of the sample. The t_{ig} for each sample was measured and recorded to the nearest tenth of a second with a stopwatch. All tests were performed with a fixed airflow velocity of 1 m/s and an irradiance of 50 kW/m^2.

We performed data analysis using the R statistical computation and graphing package (Version 2.10.1). Seasonal averages and standard deviations were calculated for foliar moisture, foliar chemistry components, and time to ignition. One-way Analysis of Variance (ANOVA) was used to determine if measured values varied significantly between the three categories. Pearson's correlations were performed to determine the relative importance of chemical allocation and foliar moisture content on time to ignition. These diagnostics helped to reduce the variables considered for further analysis. To determine how well we could predict time to ignition from both foliar moisture and chemical contents, we used the stepwise linear regression routine in R to choose the best predictor variables. The final multivariate linear model was fit, and model predictions were compared to measured time to ignition.

3. Results

3.1. Foliar moisture content

For all three sampling sites, the foliar moisture content of green, attacked, and red foliage samples varied by an order of magnitude and mean FMC values were significantly different between groups (ANOVA, $p < 0.001$, $F = 2487.2$, $n = 2642$). Red needles had the lowest mean seasonal moisture content (11.7%) and the least seasonal variation (2.3%), practically behaving as dead fuels. Green needles had the highest mean seasonal moisture content (108.5%) and moderate seasonal variation (14.1%) (Fig. 2, Table 1). The FMC for attacked trees was between that of red and green trees, and moisture content for attacked trees has the greatest seasonal variation (37.4%). Within a single growing season, the needles on attacked trees changed from green to yellow to red and at the end of the growing season, attacked tree needle moisture content was nearly the same as that of red needles (Fig. 3, Table 1).

3.2. Seasonal chemistry

The average growing-season chemical composition of green, attacked, and red needle samples is provided in Table 2. The means of each foliar chemistry allocations (NFC, NDF, fat, ash, protein)

Table 4
Correlations between time to ignition and seven intrinsic fuel characteristics across a range of conditions observed in the early stages following a MPB attack on lodgepole pine.

Variable	Correlation coefficient (ρ) and significance between variable and time to ignition
Foliar moisture content (FMC)	0.94***
Acid detergent fiber (ADF)	−0.90***
Neutral detergent fiber (NDF)	−0.92***
Non-fiber carbohydrates (NFC)	0.91***
Protein	0.28 (NS)
Fat	0.58***
Ash	−0.06 (NS)

NS = not significant.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

varied significantly between the three attack categories (ANOVA, $p < 0.05$ for ash and $p < 0.001$ for remaining four variable, $n = 48$). For healthy green needles, 83% of the total dry matter was split evenly between fiber and non-fiber carbohydrates (39.6% and 43.5%, respectively, Table 2). However, in attacked and red foliage, we observed a much smaller percentage of the dry matter in non-fiber carbohydrates (20.1–27.5%) and a much higher percentage of dry matter in structural carbohydrates (57.6–65.2%). Crude fat content was highest in green needles, lowest in recently attacked needles, and intermediate in red needles. Ash content stayed relatively constant across the attack categories (Table 2). Crude protein concentrations were roughly equal for green and attacked needles but slightly lower for red needles.

3.3. Time to ignition

Mean time to ignition varied significantly between attack categories (ANOVA, $p < 0.001$, $F = 91.268$, $n = 48$). On average, green needles took the longest time to ignite at 35.3 s and red needles ignited on average about 3 times faster at 13.3 s (Fig. 4). Strong seasonal declines in the time to ignition were measured for recently attacked trees, while slight increases were noted for both red and green trees (Table 3). Foliar moisture content, neutral detergent fiber, non-fiber carbohydrates, and crude fat were significant correlated with time to ignition (Table 4). Non-fiber (NFC) and fiber carbohydrate (NDF) allocations explained almost as much variation in time to ignition as foliar moisture content ($r^2 = 0.83$ and 0.84, respectively). Strong multicollinearity was noted between NFC and NDF (Fig. 5) and thus only NDF was selected for the final fitted model. The stepwise linear regression confirmed that foliar moisture content, NDF, and crude fat allocations were all significant variables in determining the time to ignition. A combined linear model of these three variables explained 92% of the variation in time to ignition (OLS, $p < 0.001$, $F = 158.4$, $r^2 = 0.92$, $n = 48$) (Fig. 6, Table 5).

4. Discussion

In overstory conifers, time to ignition can help to identify the minimum surface fire intensity required for a fire to carry from the surface into the crowns of trees. This minimum heating requirement has long been recognized as a significant factor in assessing the potential of a fire to transition into the canopy (Van Wagner, 1977, 1993). However, the empirical evidence supporting this early work was limited to trees with healthy, green foliage and assumed that moisture content was the most important

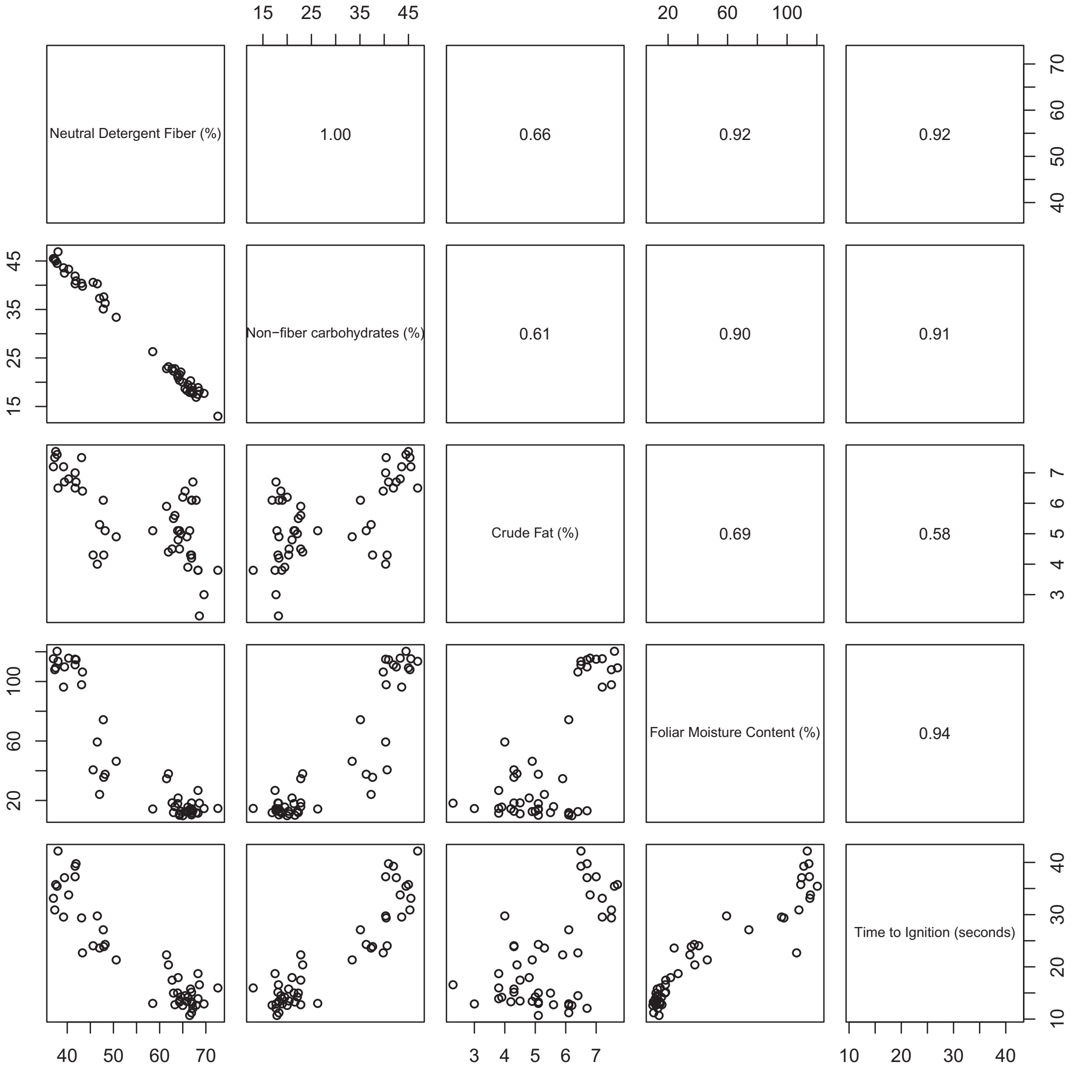

Fig. 5. Cross-correlation plots between the four most important variables and time to ignition. Pearson's correlations between each combination of variables are given in the upper half of the matrix and scatterplots for each pair are given in the lower half of the matrix. There is strong multicolinearity among some of these variables, particularly between neutral detergent fiber and non-fiber carbohydrates.

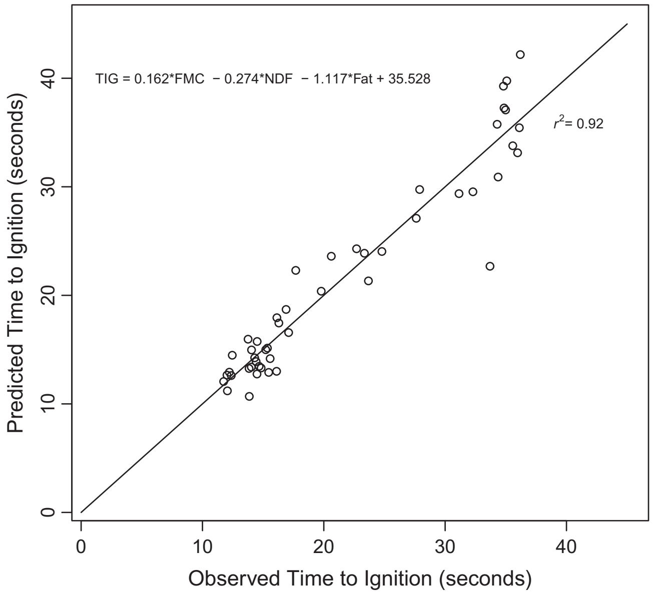

Fig. 6. Observed versus model predictions of time to ignition based on an ordinary least squares linear model using foliar moisture content, fiber carbohydrates, and crude fat as independent variables. These three variables explained 92% of the variation in the time to ignition of lodgepole pine foliage across the early attack conditions ($TIG = 0.16151 * FMC - 0.27397 * NDF - 1.11676 * fat + 35.52799$) (OLS, $p < 0.001$, $F = 158.4$, $r^2 = 0.92$, $n = 48$).

Table 5
Results of the stepwise, ordinary least squares regression model fit predicting time to ignition as a function of foliar moisture content and chemistry.

	Coefficient	Intercept	*F*-statistic	R^2
Foliar moisture content	0.16151[***]	3 5.52799	158.4[***]	0.92
Fiber carbohydrates (NDF)	−0.27397[**]			
Crude Fat	−1.11676[*]			

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

factor in determining the amount of heat required to ignite foliage. Our work is the first to experimentally assess the concurrent roles of moisture content and chemical composition on the ignition of foliage. While our results support conventional thinking that moisture content is a strong predictor in heating requirements of foliage, chemical allocation was also found to be a significant factor in determining their flammability. An improved heat of ignition criteria for crown fire initiation might include both moisture content and chemical composition as controlling variables. However, seasonal moisture content changes have been linked to seasonal chemical changes in some species (Little, 1970) and thus seasonal changes in live foliar moisture content may already reflect seasonal changes in foliar chemistry.

Fuel structure and chemical changes after a MPB attack can substantially influence expected fire behavior but the duration and extent of these changes is unclear. While we only conducted time to ignition and foliar chemistry analysis on samples from the western Montana site, patterns in fuel moisture changes following beetle attacks were similar between western Montana and Colorado sites, suggesting that time to ignition and foliar chemistry changes may also be similar. As attacked tree crowns die and their foliar moisture content decreases, their foliar flammability increases. This increase in crown flammability persists until the needles fall from the trees, a process that can take 2–3 years (British Columbia Ministry of Forests, 1995) or longer depending on site conditions. Trees at the Montana site retained most needles for 4 years after they were attacked. While we have demonstrated increased flammability with foliar desiccation, little is known about the timing and duration of post attack needle drop. This rate and timing of needle drop is likely a large factor that influences crown fire potential in attacked stands. The understanding and predictability of fire behavior in beetle-attacked stands is further complicated when surviving trees are interspersed among dead trees. The mosaic of dead and living trees may influence how the fire transitions or burns through a stand. Foliar moisture content and crown biomass, or more specifically crown bulk density, are both important factors that determine crown fire potential. Immediately following an attack, when the needles are desiccated yet still remain in the tree, crown fire potential increases. Crown fire potential diminishes as needles are gradually shed from the tree to the surface (Van Wagner, 1977).

While both moisture content and chemical content were important variables in predicting time to ignition, the high correlations between these variables makes it difficult to assess causality (Fig. 5). In most cases, changes in chemical content alone explained nearly as much of the variation in time to ignition as was explained by foliar moisture content. We included both sets of variables in our analysis despite their correlation because the nature of their information is very different, and indeed, complementary. During preheating, foliar moisture absorbs a great deal of energy because of its high specific heat and at least some of this water must be evaporated before the particle can be sufficiently heated to the point that flaming combustion can occur. At the same time, the nature and composition of the volatile gases released during the decomposition of the foliar dry matter are determined by the chemical content of the material and serve as the heat source for the flaming combustion that follows. For this reason, both aspects are relevant but determining causality is a challenge. More research is needed to truly understand the individual roles that needle chemistry and moisture play in the ignition of foliage. It is especially important to develop methods that evaluate the ignitability of fuel particles while controlling for either fuel chemistry or fuel moisture.

Fire behavior changes in mountain pine beetle-altered fuels represent a great unknown to both fire managers and scientists. While models exist to simulate these potential changes, there is a virtual void of empirical evidence to support predictions made by these models. Empirical evidence, such as observations of wildland fires burning in beetle-killed fuels, is necessary to better understand the nature and magnitude of changes we may expect to see. Intuitively, reducing the amount of heat required to ignite foliage should increase the likelihood that the crowns of attacked trees will ignite and should alter the heat released from those trees. Our results empirically demonstrate that the needles of attacked and red trees are more easily ignited than those of healthy trees and may thus pose a greater crown fire risk, as long as the physical structure of the tree remains the same. However, more work is needed to better understand the changes in fire behavior in beetle attacked stands over time in order to improve public and firefighter safety.

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