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Spruce Beetle-Induced Changes to Engelmann Spruce Foliage Flammability

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Intermountain Engelmann spruce (*Picea engelmannii* Parry ex Engelm) stands affected by the spruce beetle (*Dendroctonus rufipennis* Kirby) represent a unique and growing fuel complex. In this study, we quantified and compared the changes in moisture content, chemistry, and flammability of foliage from trees in three crown condition classes: unattacked (green [G]), currently mass attacked (green-infested [GI]), and mass attacked the previous year (yellow [Y]) over the course of a fire season. GI trees displayed highly variable decreases in moisture content both between trees and within individual tree crowns that produced variable increases in flammability. The foliage on Y trees had significantly lower moisture contents, higher proportions of lignin and cellulose, and lower proportions of carbohydrate-based compounds than G foliage, which resulted in increased flammability. This increase in crown flammability was short-lived because the foliage on Y trees dropped abruptly approximately 14 months after mass attack (by late July). Given the observed changes in flammability, increased crown fire potential may occur in spruce beetle-infested forests during the spring when G and Y foliage flammability is highest, provided sufficiently dry conditions, and in late summer when the combination of peak GI foliage flammability coincides with the peak in seasonal drying.

Keywords: crown fire, bark beetles, heat of combustion, fire behavior, time to ignition

Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* var. *latifolia* Nutt.) forests occur throughout the Intermountain region of the United States, generally above 2,400 m in elevation (Long 1994). Dense, pure stands of Engelmann spruce grow on moist, cool, high elevation sites but are often codominant with subalpine fir on drier sites at lower elevations (Alexander 1987). The primary agents of disturbance in spruce-fir forests are fire and the spruce beetle (*Dendroctonus rufipennis* Kirby [Coleoptera: Curculionidae]). Large fires are relatively rare in spruce-fir forests because of short snow-free periods and long episodes of unfavorable fire weather conditions with fire return intervals often exceeding 150 years (Arno 1980, Jenkins et al. 1998). Outbreaks of the spruce beetle occur between stand-replacing fire events as postfire stands mature (Baker and Veblen 1990), being triggered by a combination of the availability of suitable down host material (Schmid 1981) and favorable climatic conditions (Schmid and Frye 1977, DeRose and Long 2012). Outbreaks have been documented in the western United States since the mid-1880s, but mortality levels have risen sharply in recent decades (Berg et al. 2006, Hebertson and Jenkins 2008). Since 2001, spruce beetle has affected >180,000 ha of Engelmann spruce forests in the Intermountain region (Man 2010), which has caused widespread concern among land managers about the accumulation of dead forest fuels and the effects on potential fire behavior (Jenkins et al. 2008).

Recent research has quantified the influence of bark beetle-induced tree mortality on fuel complexes in several forest types common in the Intermountain West, including spruce beetle in spruce-fir forests (DeRose and Long 2009, Jorgensen and Jenkins 2011). However, it has been difficult to correlate mortality with increases in the number of ignitions, fire risk, or changes in fire behavior (Bebi et al. 2003, Kulakowski et al. 2003). Real-time fire weather, drought, and the point of ignition have all been shown to exercise greater influence on fire occurrence and extent than the prefire fuel conditions caused by spruce beetle outbreaks (Kulakowski and Veblen 2007). Current debates about the need for and appropriateness of mechanical treatments to reduce perceived fire risk in high elevation, bark beetle-attacked forests are ongoing (Black et al. 2013) and hindered by a lack of detailed information about the changes in crown fuel characteristics that influence crown fire initiation and

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spread (Hicke et al. 2012) and the inadequacy of current fire behavior models (Jenkins et al. 2012).

Although several studies have demonstrated the relatively minor influence of spruce beetle outbreaks on long-term fire risk, other work has shown that short-term changes in foliar moisture content (FMC) and chemistry in mountain pine beetle (*Dendroctonus ponderosae* Hopkins)-attacked lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.) tree crowns have the potential to alter crown fire initiation and spread (Jolly et al. 2012, Page et al. 2012). Jolly et al. (2012) in Colorado and Montana and Page et al. (2012) in Idaho demonstrated that as attacked trees die and senesce, their foliage undergoes substantial decreases in moisture content and changes in chemistry, which substantially increases foliage ignitability, mostly as a result of decreases in moisture content. Other research has also demonstrated the importance of moisture content on flammability (Van Wagner 1967a, Dimitrakopoulos and Papaioannou 2001), although the effect can decrease as the magnitude of the heat flux used in testing increases (White and Zipperer 2010). For example, using heat fluxes between 80 and 140 kW m^{-2}, Fletcher et al. (2007) found that the mass of moisture in individual leaf samples had little effect on time to ignition and ignition temperature. Fernandes and Cruz (2012) noted that peak heat fluxes in shrubland fires and crown fires in conifer forests can approach those used by Fletcher et al. (2007) and are more representative of the influence of moisture content during high-intensity fires. However, low heat flux levels representative of lower intensity surface fires and the resulting influence of moisture content may be more important when the transition from surface to crown fire is the process under consideration (Van Wagner 1977, Xanthopoulos and Wakimoto 1993).

To our knowledge, no research has been done to quantify the changes in FMC, chemistry, and flammability of Engelmann spruce affected by spruce beetle. This information is needed to improve our understanding of the effects of recent bark beetle mortality on crown fire potential (Hicke et al. 2012) and as a part of the basic fundamental research necessary to enhance current and future operational product development (Cohen 1990). As fire behavior models continue to improve by resolving more of the underlying physical processes and incorporating the spatial heterogeneity of natural fuel complexes, detailed descriptions of each of the fuel elements will be needed (Mell et al. 2009, 2010). To fill this knowledge gap and provide a better understanding of the effects of recent spruce beetle mortality on crown fuel and flammability dynamics, we quantified and compared the changes to FMC, chemistry, and flammability of foliage on Engelmann spruce trees unattacked but susceptible to attack (green [G]), currently infested (green-infested [GI]), and mass-attacked the previous year (yellow [Y]) over the course of a fire season. Based on previous research conducted in lodgepole pine forests affected by the mountain pine beetle (i.e., Jolly et al. 2012, Page et al. 2012), we hypothesized that there would be significant changes in FMC, chemistry, and flammability in both unattacked and recently attacked foliage. Specifically, as the time since attack increases, we expect FMC and soluble carbohydrates to decrease, and structural lignin and cellulose to increase in relative proportion, resulting in increased foliage flammability due primarily to decreases in FMC. In addition, we expect unattacked tree foliage to display significant changes in FMC and chemistry in response to translocation of soluble carbohydrates from old to new foliage and for GI foliage to show increases in within-needle terpene concentration and volatile emission rates due to the production of plant defensive compounds.

Methods

Study Area

USDA Forest Service Forest Health Monitoring aerial detection survey maps, consultation with local land managers, and ground reconnaissance were used to identify sites with significant levels of recent spruce beetle-caused tree mortality. The specific study site chosen was located in the western Uinta Mountains in northern Utah on the Uinta-Wasatch-Cache National Forest (40°27′47″ N, 111°7′54″ W) at an elevation of 2,987 m above mean sea level. The study site was approximately 2 ha in size with a northwest aspect and slope of 5%. Soils at the site were classified as sandy loams to loamy sands, quartzite derived, and probably nutrient poor (Briggs and MacMahon 1982). The site supported a relatively open, mixed-aged stand of Engelmann spruce and subalpine fir that was selectively harvested in the 1980s. Stand density ranged between 500 and 1,500 stems ha^{-1}, and the mean basal area was 10 to 15 m^2 ha^{-1}. The stand experienced significant spruce beetle-caused tree mortality over the previous 2–3 years (>75% of mature spruce killed) with a large increase in mortality during the summer of 2011.

Tree Selection

The foliage of eight trees in each of three crown condition classes (G, GI, and Y) for a total of 24 trees was selected for repeated sampling based on the following selection criteria: (1) similar tree characteristics in terms of size and height, (2) free from secondary disturbances, (3) adequacy of lower crown to facilitate the needs of repeated sampling, and (4) accessibility for equipment. The mean (±SE) dbh (cm), canopy base height (m), and tree height (m) of the selected trees were 26.4 ± 1.93 cm, 0.8 ± 0.08 m, and 11.7 ± 0.51 m for G, 25.5 ± 1.3 cm, 1.0 ± 0.11 m, and 13.6 ± 0.73 m for GI, and 38.5 ± 2.48 cm, 1.1 ± 0.06 m, and 17.1 ± 0.94 cm for Y, respectively. All sample trees within a crown condition class had similar sizes, but the Y trees were larger than the G or GI trees because of a host size preference during the early stages of an outbreak (Schmid and Frye 1977). Older spruce beetle-attacked trees within the study site had dropped their foliage by the time of sampling; thus, the red stage typical in other conifers attacked by bark beetles was not present. All sampling was conducted during the primary fire season in the western Uinta Mountains (June to September). In late July, the Y trees dropped all of their needles within a 2- to 3-week period. Therefore, from late July to late September only the 8 G and 8 GI trees were sampled.

Fuel Moisture and Chemistry Sampling

Fuel moisture, within-needle terpene concentration, and terpene volatile emissions were sampled from each tree twice per month. Field sampling consisted of removing approximately three 100-g samples of foliage from the lower crown of each sample tree between 1100 and 1400 hours local time at the beginning of each week. The foliar samples were returned to the laboratory where new and old needles were separated and removed from the twig material. The growth of new needles had begun by late June and made up only a small fraction of the total needles on each branch. Old foliage was considered to be all foliage attached to the twig excluding the present year's growth. About 20–30 g of foliage from each sample was weighed to the nearest 0.01 g to obtain a fresh weight and then oven-dried at 60° C for 24 hours and reweighed to obtain a dry weight. The FMC for old and new foliage was computed as the percentage of the oven-dry weight.

Field sampling of volatile terpene emissions was conducted following the procedures of Page et al. (2012) by enclosing the outer 70 cm of one branch on each tree in a clear Teflon bag and using portable automated vacuum pumps to pull air at a rate of 0.5 L minute^{-1} through volatile traps containing 30 mg of the absorbent HayeSep-Q (Restek, Bellefonte, PA). Volatile terpene emissions were collected for 30 minutes, and then the enclosed portion of branch was clipped and later weighed to obtain a fresh weight. Approximately 20−30 g of fresh foliage from each tree along with the volatile traps was immediately shipped to the Rocky Mountain Research Station in Bozeman, Montana, and stored at −80° C until processed. Within-needle terpenes were extracted from the foliage samples following the procedures used by Ormeño et al. (2009) with some modifications. Five grams of each foliage sample was ground to a fine powder in liquid nitrogen using a mortar and pestle. Approximately 0.1 g of powdered needles was transferred into 2-ml FastPrep tubes (MP Biomedicals, Solon, OH), and 1.5 ml of cyclohexane was added and sonicated at room temperature for 20 minutes. Tubes were then centrifuged at 13,000*g* for 1 minute, and 200 μl of cyclohexane (top layer) was transferred to a gas chromatograph vial for analysis. Terpene concentration and volatile emission rate were measured using an Agilent 7890A gas chromatograph coupled with a 5975C mass spectrometer; helium was used as the carrier gas. Individual compounds were identified by comparing retention times and mass spectra with appropriate internal standards. The total terpene concentration and volatile emission rate were reported on a fresh weight basis.

During the first 2 weeks of each month, approximately 60−80 g of fresh foliage from each tree was also shipped to a forage testing laboratory for chemical analysis (AgriAnalysis 2013). The chemical measures included the proportion of the sample that was lignin, cellulose, and hemicellulose, called neutral detergent fiber (NDF); the proportion composed of just lignin and cellulose (a subset of NDF), called acid detergent fiber (ADF); the proportion composed of crude fat, ash, and protein; and the remaining portion that was the starches and sugars, referred to as the nonfiber carbohydrates (NFC). A detailed listing of the procedures used to determine ADF, NDF, crude fat, and ash using the ANKOM filter bag technique, fat extractor, and ashing are detailed elsewhere (see ANKOM Technology 2013).

Flammability Testing

Each week, the old foliage collected from all trees in each condition class was subjected to flammability testing using the same setup as Page et al. (2012). In brief, a 500-W silica epiradiator was used as the heat source in conjunction with a scale, pilot flame, metal stand, and a type K thermocouple probe located approximately 1.5 cm above the sample. The thermocouple and scale were connected to a data logger that recorded the temperature and mass of the sample every 0.1 s. The sample holder was composed of a wire mesh (8 × 8 cm) placed 3 cm below the epiradiator on top of the stand. The pilot flame was located 2 cm above the top of the sample at the edge of the sample holder. Foliage was placed evenly across the holder to a depth of approximately 0.5 cm. The initial mass of the fresh samples varied from 6.3 to 10.6 g as a result of moisture differences. During each test, the sample was placed on top of the stand and the epiradiator was lowered into position. Then the time when ignition started and time that flaming ceased were recorded. The high heat of combustion was also measured for one oven-dry foliage sample taken from each tree during each week using an oxygen bomb calorimeter following ASTM D standard 1989-96 with corrections for the fuse wire, nitric acid, and aqueous sulfuric acid formed during the reaction.

Table 1. List of abbreviations, sorted alphabetically, and their units used in the article.

Abbreviation	Full name	Units
ADF	Acid detergent fiber	% of dry weight
DOF	Duration of flaming	seconds
FMC	Foliar moisture content	% oven-dry weight
G	Green foliage	
GI	Green-infested foliage	
HC	High heat of combustion	kJ kg^{-1}
HY	Heat yield	kJ kg^{-1}
$_{max}$TDF	Maximum temperature during flaming	° C
$_{maxrate}$MLR	Maximum rate of mass loss during flaming	g s^{-1}
$_{maxrate}$TDF	Maximum rate of temperature increase during flaming	° C s^{-1}
NDF	Neutral detergent fiber	% dry weight
NFC	Nonfiber carbohydrates	% dry weight
$_{prop}$MLDF	Proportion of mass lost during flaming	dimensionless
TAI	Temperature at ignition	° C
TTI	Time to ignition	seconds
Y	Yellow foliage	

Assessment of Flammability

The flammability of old foliage samples was assessed using eight different measures, two measures each of ignitability, combustibility, consumability, and sustainability (Anderson 1970, White and Zipperer 2010). Ignitability was considered to be the time to ignition (TTI) and the temperature at ignition (TAI). TTI was recorded as the time in seconds from when the thermocouple reached 60° C until flaming began (Alessio et al. 2008). TAI was the temperature of the thermocouple at ignition. Note that the thermocouple was not in contact with the sample but was 1.5 cm above it to avoid affecting the mass measurements. Combustibility was measured as the maximum temperature recorded during flaming ($_{max}$TDF) (° C) and the maximum rate of temperature increase during flaming ($_{maxrate}$TDF) (° C s^{-1}). Consumability was represented as the maximum rate of mass loss during flaming ($_{maxrate}$MLR) (g s^{-1}), using the 5-second running mean of mass loss rate to smooth the response and the proportion of total mass lost during flaming ($_{prop}$MLDF). Sustainability was considered to be the duration of flaming (DOF) (seconds) and the heat yield (HY) (kJ kg^{-1}) to account for the moisture content of the fuel. Heat yield estimates were obtained by reducing the high heat of combustion values for the latent heat absorbed when the water of reaction is vaporized and to account for the energy required to evaporate the moisture in the fuel following Van Wagner (1972) and Alexander (1982). See Table 1 for a complete listing of all abbreviations used in this article.

Historic Weather Data

Historic weather data from the Norway remote automated weather station for the period 1983−2011 were compared with the observed 2012 weather. Mean precipitation and air temperature for the spring and summer months were evaluated to compare the level of dryness during sampling with the historical average. The station was located approximately 22 km north of the study site at an elevation of 2,524 m above mean sea level. The number of years in the historical database varied for each of the months evaluated. April and May had 11 years of data, June had 12 years of data, July had 23

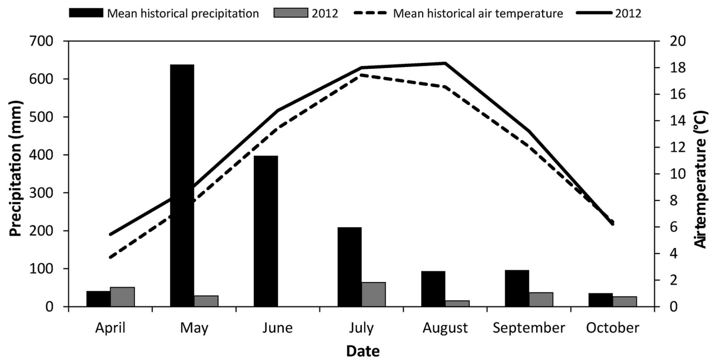

Figure 1. The mean historical (1983–2011) and 2012 precipitation and mean air temperature at the Norway remote automated weather station for the spring and summer months. The station was located approximately 22 km north of the study site at an elevation of 2,524 m above mean sea level. The number of years in the historical database varied by month: April and May, 11 years; June, 12 years; July, 23 years; August, 27 years; September, 26 years; and October, 27 years.

years of data, September had 26 years of data, and August and October had 27 years of data.

Data Analysis

Repeated-measures analysis of variance with the mixed procedure in SAS (version 9.3; SAS Institute, Inc. 2010) was used to assess differences in the mean responses of fuel moisture, chemistry, and flammability among crown condition classes and through time with crown condition class and sampling date as fixed effects. The three subsamples of old FMC from each tree were averaged to produce one value for each tree for each sampling period. The FMC, flammability, terpene concentration, and emission data were then grouped by 2-week intervals (early month and late month) for comparison. The chemistry variables (e.g., ADF and NDF) obtained from the forage testing analyses were grouped by the month in which they were sampled. Thus, for the FMC, flammability, terpene concentration, and emission data, there were eight time periods whereas the chemistry data had four time periods for comparison. Appropriate transformations were applied when necessary to meet the assumptions of normality and homogeneity of variance. The model that minimized Akaike's information criterion was used to select the proper covariance structure, which was either compound symmetry, autoregressive, or unstructured. If significant differences among the crown condition classes were found, the post hoc means comparison experiment-wise error rate was controlled using the Tukey-Kramer method.

Additional analyses using the ungrouped data were performed to evaluate the relative importance of FMC and chemistry on flammability. Specifically, because many of the flammability measures shared much of the same information, principal component analysis was used to reduce the dimensionality of the responses based on the correlation matrix. The resulting eigen values and vectors for each axis were assessed in terms of their direction, magnitude, and variability explained to determine how many dimensions to keep in the analysis. The assumption of multivariate normality was assessed by examining plots of the individual responses and applying appropriate transformations when needed. Pearson's correlation coefficients (r) were used to identify significant linear relationships between the resulting principal component scores and the original flammability responses to ascertain the principal component loadings and to interpret the importance of the individual axes. Some of the flammability observations were removed from the analysis because of incorrect readings from the data logger. The sample size for each analysis is reported in the appropriate figure or table.

To identify and correct dependence structures (serial autocorrelation) in the principal component scores and the high heat of combustion values, time series analysis using Box-Jenkins methodology (Box and Jenkins 1976) with unconditional least squares was used. Once the serial autocorrelation was accounted for, the dependence-free residuals from the appropriate autoregressive integrated moving average model were then used with multiple linear regression to identify significant linear relationships with the fuel moisture and chemistry variables, a form of two-stage regression (Durbin 1960, Tsay 1984). Stepwise selection with $\alpha = 0.15$ for entry and exit was used to select the most appropriate variables in the multiple linear regression models. We considered $\alpha = 0.05$ to indicate statistical significance, but because of the low sample sizes we also considered $\alpha = 0.10$ to indicate moderate evidence of significance. As high heat of combustion is a useful parameter for fire behavior modeling, its results are also presented separately.

Results

Foliar Moisture and Chemistry

The weather near the study site during the spring and summer of 2012 was substantially drier and slightly warmer than the historical average (Figure 1). May and June were particularly dry with precipitation between 0 and 4% of normal. Precipitation during the summer was also below average.

Beetle flight at the study site had begun by early June; thus, all three crown condition classes were available for sampling through all time periods. The observed FMCs displayed a typical seasonal pattern for new and old foliage (Figure 2). New G and GI foliage had FMCs exceeding 300% during green-up in late June followed by a gradual decrease through the end of September. The mean FMC of new G and GI foliage remained similar until September when the mean value for new GI foliage began to dip below that of G foliage, but the difference was not significant ($P = 0.4165$). The mean FMC of both old G and GI foliage was at a low of 76% in early June. The mean FMC of old G foliage reached a maximum of 107% by early September, whereas the mean FMC of GI foliage reached a high of 83% in late July and then decreased to its low of 76% again by late September. There was moderate statistical evidence suggesting that the FMC of old GI foliage was lower than that of G foliage ($P = 0.0776$) when all sampling periods were compared; however, all of

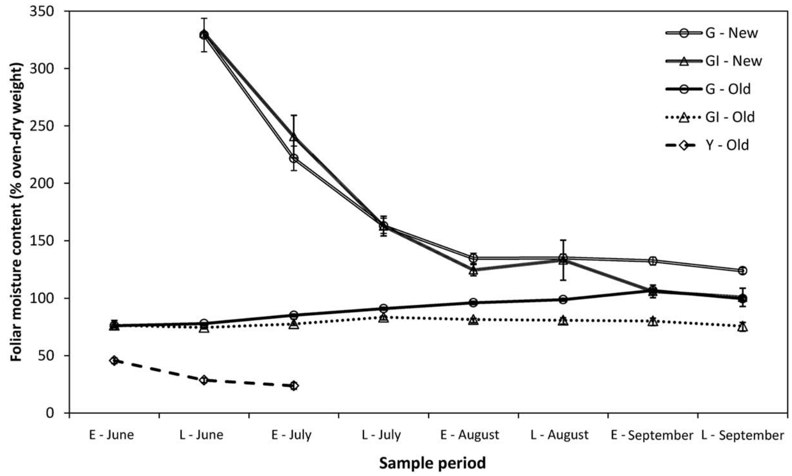

Figure 2. The seasonal change in foliar moisture content of Engelmann spruce foliage from new and old foliage on G, GI, and Y. The mean values are representative of the first 2 weeks of each month (E) and the last 2 weeks of each month (L) and are shown along with associated standard error bars (Old: G, *n* = 207; GI, *n* = 177; Y, *n* = 69) (New: G, *n* = 53; GI, *n* = 48).

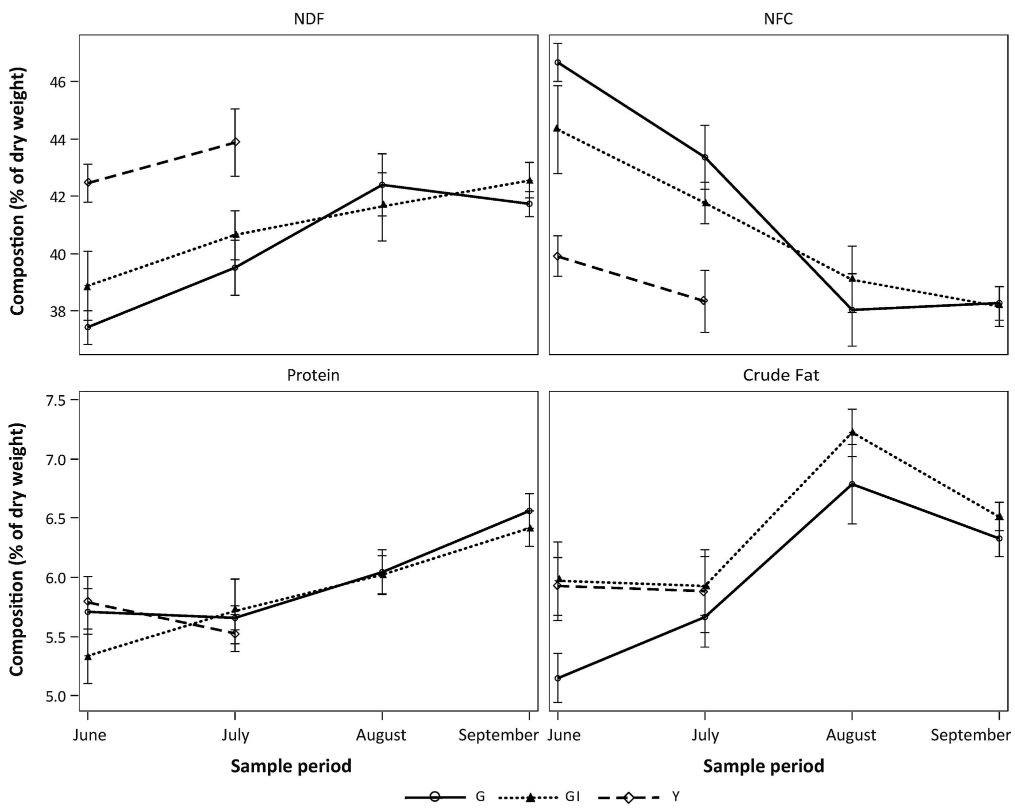

Figure 3. The seasonal change in chemical composition (June to September) of Engelmann spruce foliage from G and spruce beetle-attacked trees, either recently attacked (GI) or mass attacked the previous year (Y). The chemical composition variables were the proportion of NDF, NFC, protein, and crude fat content. The mean values are those from the first 2 weeks of each month and are shown along with associated SE bars (G, *n* = 33; GI, *n* = 31; Y, *n* = 15).

the individual sampling period comparisons were not significant ($P > 0.10$). The mean FMC of Y foliage was significantly lower than that of both G and GI foliage ($P < 0.0001$) from early June to early July, reaching a minimum of 24% in early July before the needles dropped to the ground.

The chemistry of Engelmann spruce foliage displayed significant changes both among crown condition classes and seasonally (Figure 3). The proportion of NDF increased in both G and GI foliage from a low of 37 and 39% in June to a high of 42 and 43% in September ($P = 0.036$ and $P = 0.181$), respectively. Likewise, the proportion of ADF increased from 29 and 30% in June to 33 and 34% by September for G and GI foliage ($P = 0.0007$ and $P = 0.0454$), respectively. Y foliage NDF was greater than G foliage with a mean of 42% in June ($P = 0.0045$) and 44% in July ($P = 0.0394$) but was not significantly different from that of GI foliage. The proportion of ADF in Y foliage was also greater than those of G and GI foliage with mean values of 33 and 34% in June and July ($P = 0.001$ and $P = 0.0003$), respectively. The proportion of protein among the crown

Table 2. Total volatile terpene emission rate and within-needle terpene concentration for all sample periods for each of the crown condition classes.

	G		GI		Y	
Date	Volatiles ($ng\ hr^{-1}\ g^{-1}$ fresh weight)	Within-needle (μg^{-1} fresh weightt)	Volatiles ($ng\ hr^{-1}\ g^{-1}$ fresh weight)	Within-needle (μg^{-1} fresh weight)	Volatiles ($ng\ hr^{-1}\ g^{-1}$ fresh weight)	Within-needle (μg^{-1} fresh weight)
June						
E	247 ± 31.7a	3,568 ± 1,057.5a	274 ± 31.6a	5,668 ± 1,326.9a	308 ± 48.1a	2,825 ± 1,468.6a
L	261 ± 66.9ab	3,780 ± 1,040.9a	523 ± 183.4ab	2,389 ± 772.4a	1,165 ± 592.1a	3,213 ± 1,448.0a
July						
E	492 ± 108.9ab	2,798 ± 959.3a	352 ± 74.4a	4,712 ± 1,060.5a	576 ± 127.1a	4,141 ± 1,491.0a
L	424 ± 95.7ab	5,008 ± 1,637.0a	337 ± 148.9ab	2,765 ± 770.0a		
August						
E	603 ± 251.9ab	3,987 ± 1,092.4a	492 ± 181.4ab	4,674 ± 1,239.4a		
L	742 ± 104.1b	4,423 ± 1,289.9a	607 ± 139.5ab	4,525 ± 1,134.9a		
September						
E	609 ± 148.1ab	4,104 ± 1,260.2a	675 ± 131.5b	3,325 ± 899.2a		
L	1,289 ± 535.1ab	4,635 ± 1,506.5a	1,300 ± 245.5b	3,992 ± 1,160.8a		

Data are means ± SE. Different letters within a column indicate significant differences, $\alpha = 0.10$. E, first 2 weeks of each month; L, last 2 weeks of each month.

condition classes was equivalent, but G and GI foliage displayed a significant seasonal increase from 6 and 5% in June to 7 and 6% by September ($P = 0.0014$ and $P = 0.0004$), respectively. The proportion of crude fat also increased for both G and GI foliage from 5 and 6% in June to 6 and 7% by September, but remained equivalent between each other and with Y foliage ($P > 0.10$). The proportion of ash remained equivalent among the crown condition classes and seasonally except for G foliage, which displayed a significant increase from June (5%) to September (7%) ($P < 0.0001$).

The only chemical constituent to decrease through all sampling periods was NFC. The proportion of NFC for G and GI foliage decreased from highs of 47 and 44%, respectively, in June to a low of 38% by September ($P < 0.0001$, $P = 0.0029$). The mean level of NFC between G and GI foliage remained equivalent ($P > 0.10$) for all sampling periods. The proportions of NFC in Y foliage, 40 and 38% for June and July, were significantly lower than the mean proportions for G ($P < 0.0001$) and GI foliage ($P = 0.0047$).

The total within-needle terpene concentrations were highly variable and not significantly different among crown condition classes (Table 2). Mean total terpene concentrations for G foliage did display a tendency to increase seasonally with means of 2,798 and 4,635 $\mu g\ g^{-1}$ fresh weight in early July and late September, respectively, but because of the high variability, the change was not significant ($P = 0.9702$). The emission rates of volatile terpenes for both G and GI foliage did show a stronger seasonal increase but no difference between crown condition classes (Table 2). Total emission rates were at a low in early June for G and GI foliage with mean values of 247 and 274 $ng\ h^{-1}\ g^{-1}$ fresh weight but increased to highs of 1,289 and 1,300 $ng\ h^{-1}\ g^{[1}$ fresh weight by late September ($P = 0.1847$, $P = 0.08$). Y foliage volatile terpene emission rates peaked in late June at 1,165 $ng\ h^{-1}\ g^{-1}$ fresh weight but were not different from those of G ($P = 0.9236$) or GI ($P = 0.9922$) foliage.

Flammability

There were strong linear associations among the flammability measures. The majority of the variability was accounted for by two principal component axes, cumulatively explaining approximately 66% of the total variability (46% for axis 1 and 20% for axis 2). Correlations of the first two principal component axis scores with the original flammability variables indicated that axis 1 was strongly related to all flammability measures with higher scores indicating increased flammability, i.e., lower TAI and TTI and high DOF, $_{max}$TDF, $_{maxrate}$MLR, $_{maxrate}$TDF, $_{prop}$MLDF, and heat yield (Figure 4). Axis 2 was not as strongly correlated with the flammability measures, and the resulting directions of the correlations were difficult to interpret. High principal component scores on axis 2 indicated high values of TAI, TTI, DOF, $_{max}$TDF, $_{maxrate}$TDF, and $_{prop}$MLDF, and low values of the $_{maxrate}$MLR and heat yield.

A plot of the principal component scores for axis 1 through time by crown condition class revealed significant seasonal changes as well as differences among crown condition classes (Figure 5). On this scale, Y foliage was more flammable than either G ($P < 0.0001$) or GI ($P = 0.0013$) foliage with higher scores from late June to early July. The high values were primarily attributed to increases in ignitability because Y foliage displayed significantly lower mean TTI and TAI than G ($P < 0.0001$) or GI ($P = 0.0023$) foliage. The mean TTI for G and GI foliage was 122 and 105 seconds, respectively, compared with 57 seconds for Y foliage, whereas the mean TAI for G and GI was 162 and 151° C, respectively, compared with 123° C for Y. In addition, Y foliage had significantly higher $_{maxrate}$MLR than G ($P = 0.0039$) and GI ($P = 0.039$) foliage with a mean of $0.10\ g\ s^{-1}$ compared with a mean of $0.09\ g\ s^{-1}$ for G and GI foliage.

G foliage flammability was highest in early June and subsequently decreased, reaching a low by early September ($P < 0.0001$). This trend followed observed increases in TTI ($P = 0.0001$) and TAI ($P < 0.0001$), when early June was compared with late September. The mean TTI of G foliage increased from 88 seconds in early June to 149 seconds by late September; likewise, TAI increased from 132 to 179° C from early June to late September. Significant decreases in the other flammability measures for G foliage were also observed in a comparison of mean values from early June to late September for DOF (116 versus 73 seconds; $P = 0.0232$), $_{prop}$MLDF (49 versus 34%; $P = 0.0066$), and $_{maxrate}$TDF (36.9 versus 21.3° C s^{-1}; $P = 0.0611$). The mean level of flammability for GI foliage was slightly higher than that for G foliage through the summer, but the difference was not significant ($P > 0.10$). GI foliage followed the same seasonal pattern of decreasing flammability as G foliage in a comparison of early June to late September because of increases in TTI (85 versus 139 seconds; $P = 0.0313$) and TAI (124 versus 181° C; $P = 0.0004$) and decreases in $_{prop}$MLDF (54 versus 38%; $P = 0.0327$) and $_{maxrate}$TDF (40.5 versus 20.5° C s^{-1}; $P = 0.0267$).

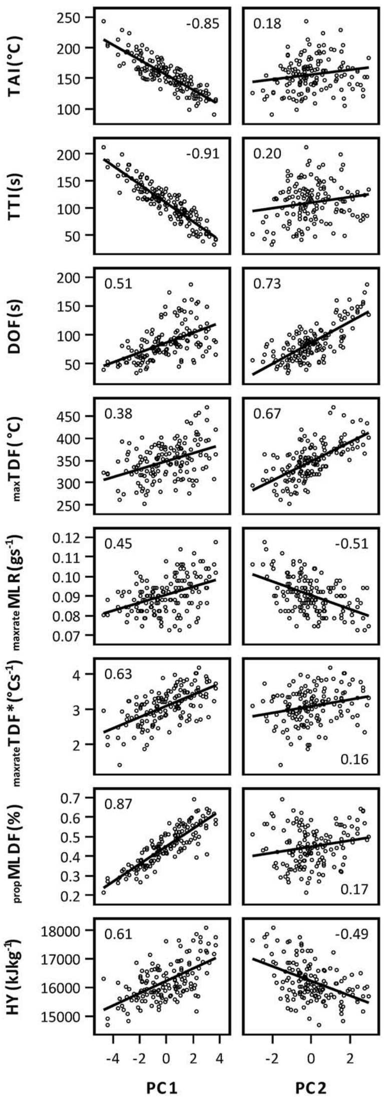

Figure 4. Correlations of principal component scores of axis 1 (PC1) and axis 2 (PC2) with the eight measures of flammability from fresh foliage: TAI, TTI, DOF, $_{max}$TDF, $_{maxrate}$MLR, $_{maxrate}$TDF, $_{prop}$MLDF, and HY. The appropriate Pearson correlation coefficient is shown in each cell. The lines are the ordinary least squares line of best fit. *, Log transformation (n = 147 for all correlations).

The dependence-free residuals from the principal component scores of axis 1 and 2 were significantly related to several variables (Table 3). The main flammability axis had a strong negative relationship with FMC, which accounted for the majority of the variability in the final model (74%). Total terpene concentration and the proportion of protein had significant positive relationships with the scores on axis 1, each explaining approximately 12% of the variability in the model. The dependence-free residuals of the scores from principal component axis 2 were significantly related to ADF, FMC, crude fat, and total terpene concentration, in descending order of variability explained in the model.

The high heat of combustion values from the bomb calorimeter testing are shown in Figure 6. Mean differences among G, GI, and Y foliage were not significant, but values for both G and GI foliage displayed significant seasonal increases. For G foliage the lowest mean value of 19,000 kJ kg^{-1} was recorded in early July, which subsequently increased to a high of 19,620 kJ kg^{-1} by late September (P = 0.0072). The lowest mean heat of combustion for GI foliage was recorded in early June (19,062 kJ kg^{-1}) and a high of 19,990 kJ kg^{-1} by late September (P = 0.0002). The mean heat of combustion for Y foliage reached a high of 19,548 kJ kg^{-1} in late June, which was slightly higher than the mean values for G or GI foliage, but the difference was not significant.

Multiple linear regression of the dependence-free residuals of high heat of combustion with the chemistry variables indicated that the proportions of ADF, ash, and total terpene concentration were significantly related to the high heat of combustion (Table 4). Ash and total terpene concentration explained the highest proportion of variability in the model (52 and 35%, respectively), whereas ADF explained the least (9%). Both ADF and total terpene concentration were positively related to high heat of combustion, whereas the proportion of ash had a negative association with high heat of combustion.

Discussion

Spruce Beetle-Induced Changes to Foliar Moisture and Chemistry

Engelmann spruce trees mass attacked by spruce beetle displayed substantial decreases in FMC with the magnitude of the decrease being dependent on the time since attack. In absolute terms, the FMC of Y foliage was 59% lower than that of G foliage, reaching a low mean value of 24% by early July, which was also the time when the lowest FMC on an individual tree was observed at 7%. This finding is similar to that for Y foliage on lodgepole pine attacked by the mountain pine beetle in Idaho, which had a mean FMC of 24% for the period July through September (Page et al. 2012). The changes in FMC in old GI foliage were not as substantial, with the greatest mean absolute difference of 27% observed during early September. This finding contrasts with similar work completed by Jolly et al. (2012), who observed decreases in FMC of old GI foliage from lodgepole pine that had been mass attacked by mountain pine beetle, but is consistent with the work of Page et al. (2012), who failed to find a significant drop in FMC of old GI foliage on lodgepole pine. Although the mean FMC of old GI foliage in our study did not substantially decrease, the observed values were highly variable among trees and among samples collected from individual trees. At different periods over the course of the fire season, the FMC collected from various portions of GI tree crowns differed, in absolute terms, by as much as 43%. The extent of larval feeding as influenced by the rate of maturation (Wermelinger and Seifert 1998) and/or the rate of blue stain (*Ophiostoma* spp.) (Krokene and Solheim 1998) development might have accounted for the variability observed as well as microsite factors such as water uptake, competition, and genetic variability. Schmid (1976) observed similar variations in individual tree crowns of recently attacked Engelmann spruce, noting that in otherwise green crowns, clusters of needles died and turned yellowish-green (presuming a decrease in FMC) before dropping to the ground.

The differences in the chemistry of Y foliage followed the expected pattern of lower starches and sugars and higher proportions of lignin, cellulose, and hemicellulose compared with those of unattacked foliage. Both Jolly et al. (2012) and Page et al. (2012) observed analogous chemical changes in mountain pine beetle-attacked lodgepole pine foliage, reflecting a shift in composition from the soluble carbohydrate compounds to the structural components of lignin and cellulose. Other work studying the rate of litter decomposition has also shown increased concentrations of lignin as decomposition progresses (Edmonds 1980), which is attributed to the

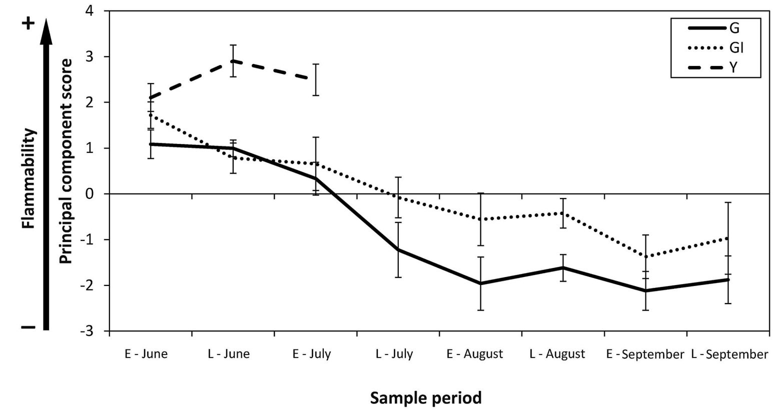

Figure 5. Plot of principal component scores through time by crown condition class from axis 1 of the principal component analysis of old foliage flammability. Higher scores indicate higher flammability. The mean values are representative of the first 2 weeks of each month (E) and the last 2 weeks of each month (L) and are shown along with associated SE error bars (G, *n* = 67; GI, *n* = 58; Y, *n* = 22).

Table 3. Results of multiple linear regression of the dependence-free residuals of the old foliage principal component scores on axis 1 and 2 with the fuel moisture and chemistry variables using stepwise selection.

Variable	Estimate	SE	*t* value	$P > t$	SS (% total)	RMSE	Adjusted R^2
Principal component axis 1 scores						1.04	0.44
Intercept	−0.2	1.2	−0.16	0.8727	1.7		
FMC (% oven-dry weight)	−0.04	0.005	−7.46	<0.0001	74.4		
Protein (% of dry weight)	0.5	0.2	2.2	0.0307	11.7		
TC (ng g^{-1} fresh weight)	1.1E−07	3.9E−08	2.77	0.0071	12.3		
Principal component axis 2 scores						1.03	0.22
Intercept	3.9	1.6	2.54	0.0134	0.3		
FMC (% oven-dry weight)	0.02	0.005	3.17	0.0022	30.9		
ADF (% dry weight)	−0.1	0.05	−2.09	0.0399	40.7		
Fat (% oven-dry weight)	−0.3	0.2	−2.28	0.0256	16.5		
TC (ng g^{-1} fresh weight)	6.6E−08	3.9E−08	1.71	0.0918	11.5		

Estimates of variable coefficients are given along with the SE, *t* values, and the proportion of variability explained by that variable using type I sums of squares (SS). The goodness-of-fit statistics of root mean square error (RMSE) and the adjusted R^2 are also given. The final models included FMC, ADF, protein, crude fat, and total terpene concentration (TC) ($n = 76$).

breakdown of the soluble carbohydrates and a decrease in volatile compounds as needles age.

Contrary to our initial expectations, we did not find differences in terpene concentration and emission rate between G and GI foliage. Terpenes are known to have inhibitory effects on bark beetle and blue stain development (Raffa and Smalley 1995, Zhao et al. 2011), indicating that trees use these chemicals as a defense against bark beetle attack (Franceschi et al. 2005). Although other research has documented increases in terpenes in spruce boles after inoculation with blue stain (Zhao et al. 2011), we only found seasonal increases in terpene emission rate and concentration in both G and GI foliage. This finding suggests that increases in terpenes in tree boles caused by bark beetle attack may not manifest into increases in tree foliage.

The rapid loss of foliage on Y trees was initially unexpected. Schmid (1976) reported that the needles of Engelmann spruce in Wyoming remained attached for up to 3 years after attack and displayed a gradual loss over that time period. In this study, the vast majority of needles on Y trees (>75%) dropped over a 2- to 3-week period about 14 months after the attack, which did not appear to be associated with any single weather event. Massey and Wygant (1954) also reported that the needles of infested Engelmann spruce in Colorado fell after approximately 1 year. In addition, research summarizing needle retention after harvest on spruce slash also suggested that needle longevity on branches was near 1 year (Salazar and Bevins 1984).

Seasonal Changes in Foliar Moisture and Chemistry

The observed seasonal change in FMC of old G foliage corresponded to changes observed in other conifers in North America (Keyes 2006) and Engelmann spruce in New Mexico (Gary 1971). Gary (1971) recorded the lowest FMC in 1-year-old Engelmann spruce foliage in June after bud burst with values ranging between 80 and 90% and the highest value of 130% in September. In this study the lowest and highest mean FMCs were also recorded in early June and early September (76 and 107%, respectively); however, mean FMCs were generally lower than those reported in Gary (1971). The atypically dry spring and summer conditions that prevailed in the western Uintas at the time of sampling may explain this difference. Combining all of the non-new foliage ages into one class may provide another explanation because older foliage generally has lower FMCs (Hatcher 1990).

As expected, there was a seasonal decrease in the proportion of old G foliage composed of carbohydrates. According to Gary (1971), who observed a decrease in the dry weight of 1-year-old foliage, carbohydrate translocation from reserves in old foliage to new foliage may be the primary cause. Other work has also noted a seasonal change of dry weight in various tree species including balsam fir (*Abies balsamea* L. Mill.) (Little 1970) and other gymnosperms (Kozlowski and Clausen 1965) with most suggesting that the mechanism is the reallocation of carbohydrates during the growing season.

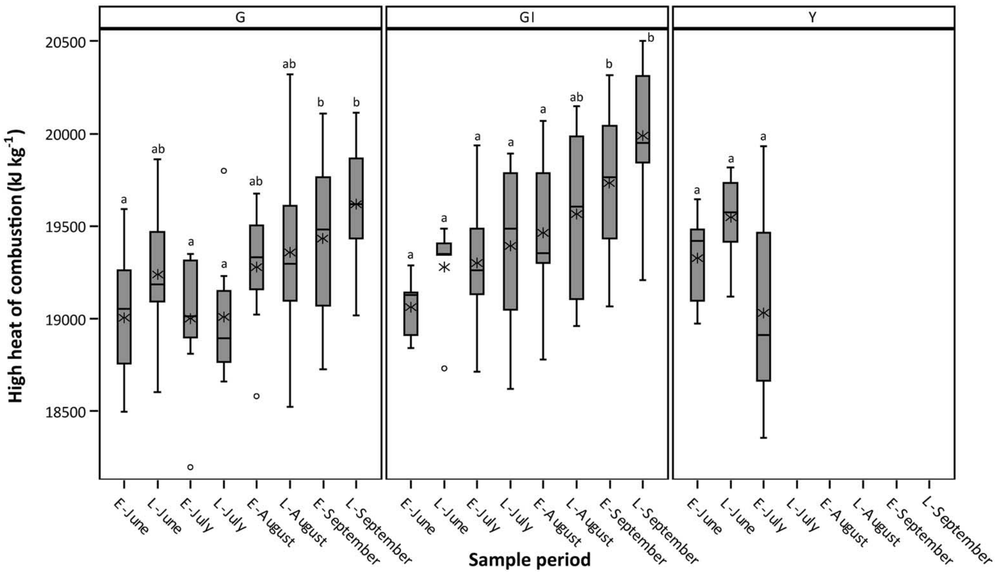

Figure 6. Box and whisker plots for the measured high heats of combustion of Engelmann spruce foliage during the fire season from G, GI, and Y trees. The values are representative of the first 2 weeks of each month (E) and the last 2 weeks of each month (L). The mean is the asterisk, the median is the horizontal line, the ends of the boxes are the first and third quartiles, and outliers are more than 1.5 times the interquartile range. Different letters within a crown condition class indicate significant differences, $\alpha = 0.10$ (G, $n = 69$; GI, $n = 59$; Y, $n = 23$).

Table 4. Results of multiple linear regression of the dependence-free residuals of high heat of combustion with the chemistry variables using stepwise selection.

Variable	Estimate	SE	*t* value	$P > t$	SS (% total)	RMSE	Adjusted R^2
Intercept	−513.1	487.4	−1.05	0.2959	3.6	323.2	0.32
ADF (% dry weight)	34.6	14.6	2.37	0.0202	8.7		
Ash (% dry weight)	−133.5	34.5	−3.87	0.0002	52.3		
TC (ng g^{-1} fresh weight)	0.00004	0.00001	3.81	0.0003	35.4		

Estimates of variable coefficients are given along with the SE, *t* values, and the proportion of variability explained by that variable using type I sums of squares (SS). The goodness-of-fit statistics of root mean square error (RMSE) and the adjusted R^2 are also given. The final model included ADF, ash, and total terpene concentration (TC) ($n = 79$).

Changes in Flammability

Spruce beetle-affected trees displayed substantial increases in flammability compared with unattacked trees. Old Y foliage was more flammable than either old G or GI foliage, exhibiting increases in foliage ignitability and consumability, due primarily to decreases in FMC. In addition, old GI foliage was slightly more flammable than G foliage, being dependent on the highly variable changes in FMC within individual tree crowns. Besides the anticipated importance of FMC on flammability, we also found that foliar chemistry, particularly the proportions of lignin, cellulose, and extractives (crude fat and terpene concentration) were important predictors of flammability. Carbohydrates and compounds such as crude fat, resins, and waxes are known to play an important role in plant flammability because they are less thermally stable and more volatile and have lower boiling points than the structural compounds of lignin and cellulose (Richards 1940, Philpot and Mutch 1971, Shafizadeh 1971). Plant terpenes have also been suggested to have a significant role in both litter flammability (Ormeño et al. 2009) and at larger scales where they may enhance the potential for explosive fire behavior (Chetehouna et al. 2009). The structural compounds of lignin and cellulose were also found to be more strongly related to high heat of combustion. Rothermel (1976) proposed a model for predicting heat of combustion of forest fuels based on the amount of lignin, cellulose, ether extractives, and ash, which is nearly identical to that for the compounds we identified as significantly related to our heat of combustion values.

Implications for Crown Fire Potential

The interpretation of the changes in FMC, chemistry, and resulting flammability described above suggest periods of increased crown fire potential in recently attacked stands. However, as with any fire behavior assessment, site-specific fuel and weather information is needed to make an accurate fire behavior forecast (Rothermel 1983). Assuming all else equal, there exists the potential that stands containing high proportions of the spruce beetle-altered foliage would be vulnerable to changes in crown fire initiation due to the relatively high ignitability of foliage, particularly during periods when surface fire behavior and/or canopy base height would otherwise limit crown fire development, such as under moderate fire weather or at the beginning or end of the burn period. This increase in crown fire potential, relative to that of stands containing no mortality, may be short-lived and dependent on the relative proportion of trees in each crown condition class. If the majority of attacked trees are in the Y class and mixed with G trees, there would be a substantial but relatively small window of increased crown fire potential during the spring coinciding with minimums of FMC in Y and G foliage. This peak in crown fire potential in the spring has been suggested by others (Van Wagner 1967b) and has been linked to the observed dip in FMC that occurs during this period. The period of increased crown fire potential would last until late July by which time most of the Y foliage would have fallen to the ground, resulting in decreased canopy fuel density and continuity. However, as noted by Schmid (1976), there may be cases when the needles are retained for longer periods of time, which may extend the period of increased crown fire potential. Once the needles do fall, subsequent increases in shrubs and forbs in the understory over the next few years may further decrease crown fire potential (Kulakowski et al. 2003, Jorgensen and Jenkins 2011). Where there are substantial proportions of GI trees or stands with mixtures of crown condition classes, another peak in crown fire potential is likely to occur by September due to decreases in FMC on GI trees coupled with normal seasonal drying of the surface fuels.

The proposed changes in crown fire potential should be considered in the context of where these forests occur. It is well accepted that the interval between large fires in these forests are long and that extended dry periods are needed for large fire growth (Arno 1980, Williams and Rothermel 1992). In addition, most research to date has suggested that the long-term impact of spruce beetle-caused tree mortality on fire risk in spruce-fir forests may largely be overestimated (Schmid and Frye 1977, Bebi et al. 2003). In light of this fact, the influence of spruce beetle outbreaks on crown fire potential may not be of great or frequent ecological significance but is important to wildland firefighters in an operational setting. When conditions are suitable for fire spread in these forests, firefighters may be faced with situations in stands with high levels of recent mortality where unexpected transitions to crown fire could occur under more moderate fire weather and into the evening or early morning hours. Rapid and/or unexpected shifts from a surface fire to a crown fire pose potential safety risks to firefighters due to increases in fire line intensity that can, in turn, affect spotting potential and safety zone size (Butler and Cohen 1998, Jenkins et al. 2012). The changes might also become more important as large fire frequency increases because of projected increases in temperature and drought in the western United States (Westerling et al. 2006, Intergovernmental Panel on Climate Change 2007, Seager et al. 2007).

Conclusion

Although previous research has demonstrated the importance of FMC, chemistry, and resulting flammability on estimating crown fire potential (e.g., Van Wagner 1977), only recently have attempts been made to measure these variables in stands recently attacked by bark beetles (Jolly et al. 2012, Page et al. 2012). Both Cruz and Alexander (2010) and Jenkins et al. (2012) noted the substantial limitations of current models used to predict crown fire initiation in bark beetle-attacked stands and the need for quantifying these changes to make accurate assessments of crown fire potential. Computationally intensive physics-based models that can incorporate spatially explicit heterogeneity in crown fuels will need this information as they become more reliable with continued validation and evaluation (Mell et al. 2009, Alexander and Cruz 2013). The work presented here is an important step to fully understanding the range of potential interactions between bark beetle-caused mortality and subsequent fire behavior. As Hicke et al. (2012) noted, there is currently a gap in our understanding of bark beetle-fire interactions during the early stages of attack. The results provided here will help close that gap and provide important information to fire managers and fire behavior modelers.

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