Research Note

Seasonal relationships between foliar moisture content, heat content and biochemistry of lodgepole pine and big sagebrush foliage

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Abstract. Wildland fires propagate by liberating energy contained within living and senescent plant biomass. The maximum amount of energy that can be generated by burning a given plant part can be quantified and is generally referred to as its heat content (HC). Many studies have examined heat content of wildland fuels but studies examining the seasonal variation in foliar HC among vegetation types are severely lacking. We collected foliage samples bi-weekly for five months from two common species in the western USA: lodgepole pine (*Pinus contorta* Douglas ex Loudon) and big sagebrush (*Artemisia tridentata* Nutt). We measured HC, live fuel moisture content (LFMC) and biochemical components in the leaf dry mass. Our results showed that HC increased for both species, coinciding with LFMC decrease during the growing season. Measured HC values were higher than the constant value in standard fuel models. Lasso regression models identified biochemical components for explaining temporal HC and LFMC variation in lodgepole pine (HC: $R^2_{adj} = 0.55$, root mean square error (RMSE) = 0.35; LFMC: $R^2_{adj} = 0.84$, RMSE = 10.79), sagebrush (HC: $R^2_{adj} = 0.90$, RMSE = 0.13; LFMC: $R^2_{adj} = 0.96$, RMSE = 7.66) and combined data from both species (HC: $R^2_{adj} = 0.77$, RMSE = 0.33; LFMC: $R^2_{adj} = 0.61$, RMSE = 19.75). These results demonstrated the seasonal change in HC and LFMC resulted from temporal biochemical composition variation in dry mass. This new knowledge about HC seasonal change will ultimately lead to improved predictions of wildland fire spread and intensity.

Additional keywords: biochemistry, fuel heat content, live fuel moisture content.

Introduction

Heat of combustion, or simply heat content (HC), is defined as total heat released from combustion per unit dry mass (MJ kg^{-1}). HC is directly related to fuel flammability (Anderson 1970). Fire behaviour models use fuel models to categorise fuel types (Rothermel 1972; Albini 1976; Burgan and Rothermel 1984; Finney 1998; Andrews *et al.* 2003), and standard fuel models use a standard value of 18.61 MJ kg^{-1} of HC. These fuel models have worked well for predicting surface fire spread rate and intensity of active fires at the peak of the fire season in part because the associated dry conditions lead to a more uniform fuel complex, an important assumption of the underlying fire spread model (Scott and Burgan 2005). Several studies have specified HC variation at greater precision for Sierra Nevada conifer species (Van Wagdendonk *et al.* 1998), Mediterranean species (Dimitrakopoulos and Panov 2001), interior Pacific North-west conifer foliage in the US (Williamson and Agee 2002), invasive and native plants in the north-eastern US (Dibble *et al.* 2007) and upland pine savannas of the south-eastern

US (Reid and Robertson 2012). These studies have quantified HC of foliage for a single point in time; no study has examined its seasonal variation.

Another key component of foliage flammability is live fuel moisture content (LFMC). LFMC is defined as the ratio of water content to dry matter content in live fuel. The popularity of LFMC as a measure of fire danger stems from its use as an input to the Rothermel (1972) model of surface fire spread rate. Fuel models used in the Rothermel-type fire behaviour and fire spread models typically assume that dry mass does not change over time, and that the HC of dry mass is constant over time and across species. However, plant physiology studies have demonstrated seasonal variation in dry mass, such that temporal variation in LFMC can be due to changes in both water mass and dry mass. Jolly *et al.* (2014) demonstrated that changes in dry matter exerted a stronger control on seasonal LFMC dynamics than actual changes in water content in lodgepole pine (*Pinus contorta*). Qi *et al.* (2014) also found that changes in water and dry mass made a similar contribution to LFMC

seasonal change in big sagebrush (*Artemisia tridentata* Nutt). Dry mass changes are a function of the physiological development of new foliage and the photosynthetic accumulation and depletion of stored carbon of both old and new foliage; thus foliar biochemistry presumably results in HC and LFMC variation. It is still unclear how biochemical variation contributes to temporal HC variation and how LFMC correlates with HC. Thus it is important to examine the biochemical foundations of dry mass seasonality coinciding with HC and LFMC.

To further our understanding of interactions between seasonal changes in foliage HC, LFMC and biochemistry, we intend to answer three research questions in this study: (1) How does foliar HC change over time? (2) What is the relationship between foliar HC and LFMC? (3) How does foliar biochemistry drive seasonal HC and LFMC variation? We collected foliage samples from two species and measured HC, LFMC and biochemical components during the growth season in 2012. We examined the seasonal variation and explained temporal HC and LFMC variation based on foliar biochemistry.

Data and methods

Study area

We studied two common species in the Western US: lodgepole pine (*Pinus contorta* Douglas ex Loudon), an evergreen needleleaf tree species, and big sagebrush (*Artemisia tridentata* Nutt), a semi-deciduous broadleaf shrub species. We collected field samples at two lodgepole pine sites in natural conifer forest and two big sagebrush sites near Missoula, Montana between July and October, 2012. The two lodgepole pine sites were in natural conifer forest on south slopes at elevations averaging 1330 and 1590 m. The two sagebrush sites were on flat natural shrubland adjacent to mixed conifer forests at elevations of 1133 and 1226 m. Current-year pine needles began to emerge in early June and elongated until the end of the growth season. Sagebrush showed a flush of new leaves in late May. We sampled all four sites once per week using a random sampling scheme to include a large number of individuals from each species. We separately sampled current year ('new') and second year and older ('old') lodgepole pine needles. Sagebrush branch tips (3–5 cm) were collected to represent new growth. About 40 g of foliage were collected and mixed from each site on the sampling day, and then stored in sealed plastic bags in a cooler with ice. Each 40-g sample was then divided into sub-samples for HC, LFMC and foliar chemistry measurements.

HC and LFMC measurements

Approximately 0.3 g of oven dried pine needles and sagebrush leaves were burned in an IKA 200 oxygen bomb calorimeter (IKA-Werke GmbH & Co., Staufen, Germany) to measure HC $(MJ\,kg^{-1})$, and the average of three measurements was recorded for each site on the sampling date. LFMC was measured for 12 groups of five needle fascicles and 12 sagebrush branch tips at each site. Fresh mass was determined within 4 h after collection, and then samples were dried in a convection oven for 24 h at a temperature of 95°C and re-weighed. The difference between fresh mass and dry mass was used to determine water mass, and LFMC was calculated by dividing the water mass by dry mass.

Biochemistry measurements

We used ~20 g of foliar samples for biochemical component measurements by AgriAnalysis Forage Analysis Laboratory (http://www.agrianalysis.com; Leola, PA, USA). Wet chemistry analysis was used to determine neutral detergent fibre (NDF, including lignin, cellulose and hemicellulose), non-structural carbohydrates (NSC, mainly starch and sugar), neutral detergent soluble fibre (NDSF, including pectin, β-glucan, galactan, and fructan), crude protein (CP, such as nitrogen-bearing content and rubisco), crude fat (CF, including isoprenoid, essential oil, wax and other lipid) and ash content (AC) as a percentage of dry mass.

Statistical analysis

We constructed lasso regression models between foliar biochemical components as independent variables and HC and LFMC as dependent variables for individual species. Lasso regression is a useful shrinkage and variable selection method to generate linear models for estimating dependent variables (Tibshirani 1994; Friedman *et al.* 2010). The lasso method has advantages over least-squares methods (e.g. stepwise regression) because it reduces the variance of prediction and conducts variable selection, which ridge shrinkage regression do not support (James *et al.* 2013). Lasso regression requires a λ-value to formulate a lasso penalty function to select variables and calculate coefficients. We conducted *n*-fold cross-validation on the observed data from each species to identify the critical λ-value for which the estimation error was smallest. Then the model was re-fit using this critical λ-value. We also constructed a model on the combined data from the two species using the prior knowledge from individual models. Finally, we examined the relationship between HC and LFMC for each species.

Results

In total we conducted 239 HC and 1238 LFMC measurements for two species. The mean and standard deviation were 20.87 and 0.78 $(MJ\,kg^{-1})$ in HC and 143.83 and 62.14 (%) in LFMC. The average HC of new pine needles at the two sites increased from 20.2 to 21.4 MJ kg^{-1} and of sagebrush, from 19.0 to 20.6 MJ kg^{-1} (Fig. 1*a*). The HC of old pine needles remained relatively stable between 20.8 and 21.8 MJ kg^{-1}. The HC of new needles converged on that of old needles at the end of the growth season. The average LFMC of lodgepole pine needles at the two sites was 202% in mid-July when new growth started to emerge (Fig. 1*b*). As the needles developed, LFMC decreased to 121% in mid-October. Sagebrush began with a high LFMC (239%), which dropped to 71% at the end of September. The LFMC rate of decrease over time slowed at the end of the sampling period. Biochemical measurements averaged over the two sites for each species described a seasonal trend (Fig. 2). CF significantly increased during the study period from 2% to 6% in the new needles and from 4% to 6% in sagebrush leaves. NSC increased in both new pine needles and sagebrush leaves throughout the season. NDF comprised the largest proportion of dry mass in samples. It decreased in new lodgepole pine needles but stayed relatively stable in old needles and sagebrush leaves. CP and AC decreased in sagebrush leaves and showed slight fluctuation in pine needles.
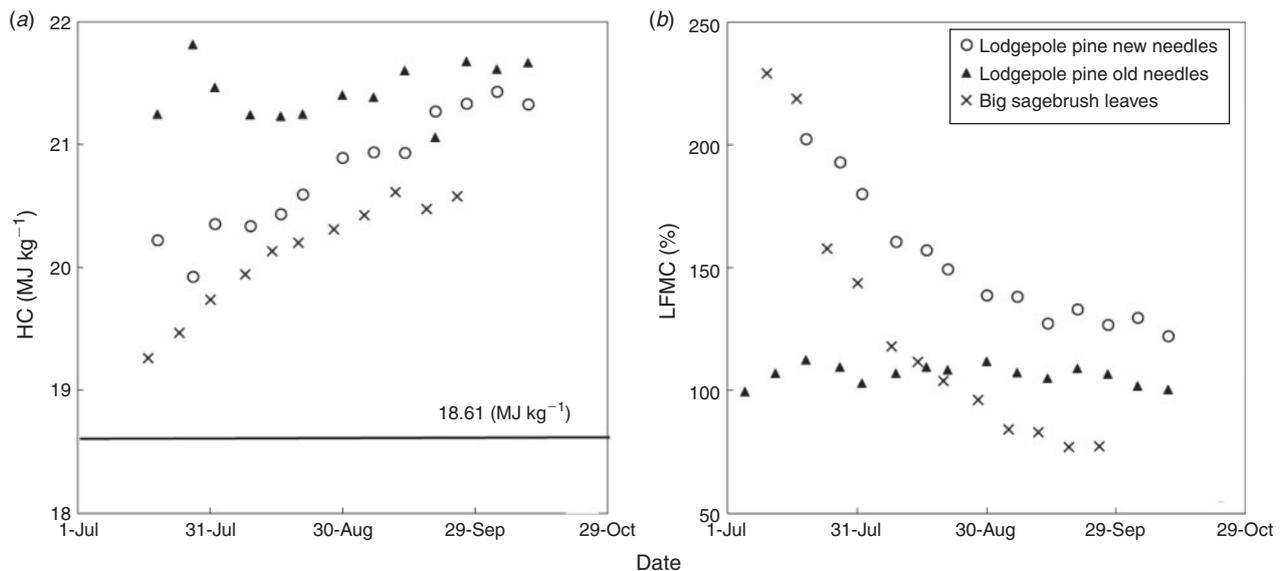
Fig. 1. (*a*) Seasonal trends of average heat content (HC) at the two study sites for lodgepole pine new and old needles, and big sagebrush leaves. The solid line represents the standard HC value of 18.61 MJ kg^{-1} (8000 BTU lb^{-1}) in Albini (1976). (*b*) Seasonal trends of average live fuel moisture content (LFMC) at the two sites for lodgepole pine new and old needles, and big sagebrush leaves.

HC and LFMC were negatively correlated in both lodgepole new needles and sagebrush leaves (Fig. 3). The R^2_{adj} of linear regression between HC and LFMC was 0.78 for lodgepole pine new needles and 0.89 for sagebrush leaves. Lodgepole pine generally had higher HC than big sagebrush when they presented similar LFMC. For example, pine and sagebrush showed 21.1 and 19.8 MJ kg^{-1} HC, at 133% of LFMC.

Lasso regression models selected biochemical components as predictors to estimate HC and LFMC (Table 1). CF, NSC and NDF explained 54% of the variance in lodgepole pine HC; CF, NSC and AC explained 90% of the variance in sagebrush HC. CP and NDSF were not selected for either species model, so were excluded prior to building the cross-species model, which identified CF, NSC and AC with R^2_{adj} of 0.77. CF and NSC presented positive coefficients with HC in all models. As for LFMC, individual species models selected different components and produced higher R^2_{adj} than HC models. Protein was selected in individual species but not in the cross-species model, which was likely due to the larger variance of LFMC in the combined dataset. CF and NSC were negatively correlated predictors in all LFMC models.

Discussion

Our study adds new empirical evidence about temporal HC variation for conifer and shrub species. Observed HC for both lodgepole pine and big sagebrush were always larger than the standard value of 18.61 MJ kg^{-1} used in fuel models (Scott and Burgan 2005) and lower than in previous literature (22.84 MJ kg^{-1} in lodgepole pine, Van Wagdendonk *et al.* 1998). The increasing trend of HC in lodgepole pine new needles and big sagebrush challenged the presumption of constant HC over time. Lodgepole pine generally had larger HC than big sagebrush at similar LFMC, as lodgepole pine needles had more CF than big sagebrush leaves.

Some studies have considered the effects of CF (Philpot 1969; Owens *et al.* 1998), moisture content, ash and extractive content (Demirbas 2002, 2007) on foliar heat content, but no study has comprehensively considered the differences in foliar biochemical composition in association with seasonal HC variation. Our results agreed with previous literature on NSC and CF as major biochemical drivers of LFMC change in lodgepole pine and sagebrush foliage (Jolly *et al.* 2014; Qi *et al.* 2014). More importantly, our study identified CF and NSC as significant predictors for HC in both species. CF includes extractive materials such as isoprenoid, essential oil, wax and other lipids. These compounds collectively contain about twice the HC of other fuel components (Philpot 1969). In our samples, CF tripled from 2% to 6% of dry mass in lodgepole pine new needles from July to October. The seasonal increase of CF in foliage is partly responsible for the increase in the HC of fuels. NSC and CF had positive coefficients in HC models and negative coefficients in LFMC models. This explained the negative linear relationship between HC and LFMC.

HC has been shown to positively influence plant flammability (Van Wilgen *et al.* 1990; Rodriguez-Añón *et al.* 1995; Owens *et al.* 1998). Lodgepole pine needles live an average of 4–6 years. Although the proportion of new needles depends on the growth and defoliation rate, new needles could presumably account for 16–25% of total foliage. The seasonal increase of HC in new needles would likely increase total HC in fuel, which would increase the fuel flammability and higher heat release rate; thus nearby unburned fuel ignites faster, leading to increased spread rate. It is known that actual energy release and fireline intensity depends on multiple fuel properties besides HC. HC measured using a bomb calorimeter is usually larger than the effective heat of combustion in the field (Babrauskas 2006). LFMC is also an important fuel property to determine fire spread and intensity (Rothermel 1972). The observed covariation between LFMC and
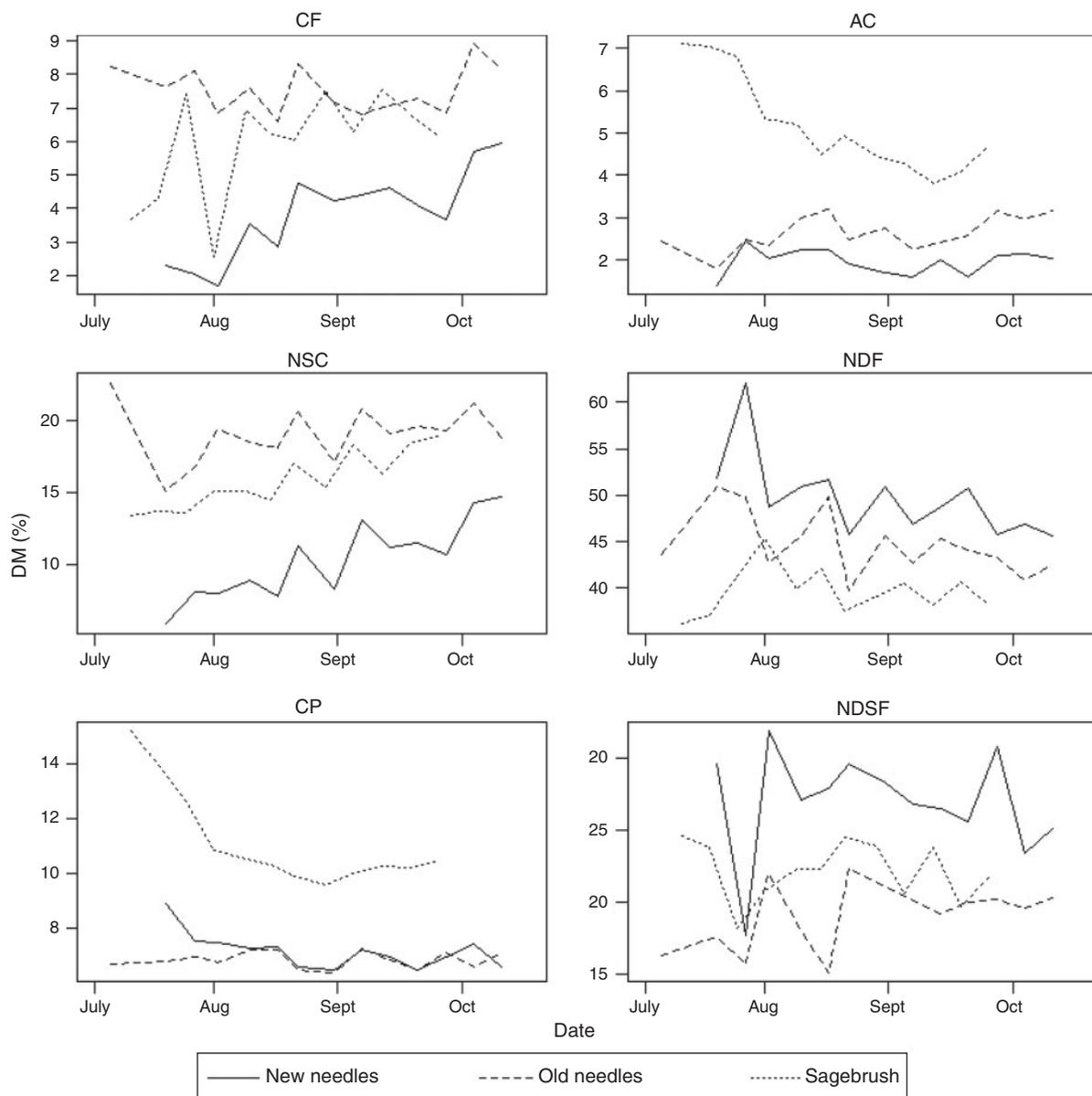
Fig. 2. Seasonal variation of averaged foliar biochemical components in lodgepole pine needles and big sagebrush leaves at the two sites between July and October 2012. DM, dry mass; CF, crude fat; AC, ash content; NSC, non-structural carbohydrates; NDF, neutral detergent fibre; CP, crude protein; NDSF, neutral detergent soluble fibre.

HC in this study is not currently integrated into existing fire behaviour models. Further research is needed to establish the effect of temporal HC variation on fuel flammability and fire behaviour. Recent studies have used remote sensing to monitor seasonal LFMC and biochemical variation (Qi *et al.* 2014). As HC was directly associated with biochemical variation and expressed a nearly linear relationship with LFMC, future work will need to investigate the possibility of spectral estimation of HC.

Conclusions

This research examined the seasonal variation in HC and LFMC of lodgepole pine and big sagebrush foliage. Our results showed that HC of lodgepole new needles and sagebrush leaves increased over time, and the HC of both species was higher than the standard value currently used in fuel models. Coinciding with this, LFMC demonstrated a negative linear relationship with HC. The seasonal HC and LFMC variation was attributed to the biochemical component changes in dry mass, specifically the CF and NSC, which showed positive correlation with HC and negative correlation with LFMC in both individual species and cross-species models. Our methodology could be applied to a range of plant types to estimate HC variation. These results will improve existing understanding of temporal variation and biochemical dynamics in HC, and this new knowledge will ultimately lead to improved predictions of wildland fire spread and intensity.
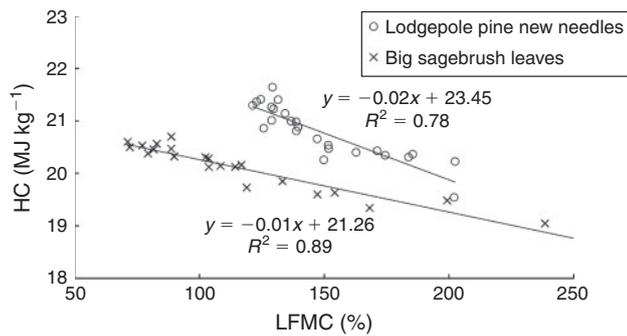
Fig. 3.   Relationship between live fuel moisture content (LFMC) and heat content (HC) of lodgepole pine new needles and big sagebrush leaves.

Table 1.   Summary of lasso regression models for estimating foliar heat content (HC) and live fuel moisture content (LFMC) as a function of foliar biochemical components, including adjusted *R* square (R^2_{adj}), root mean square error (RMSE), variable coefficients and model intercept

NDF, neutral detergent fibre; NSC, non-structural carbohydrates; CP, crude protein; CF, crude fat; AC, ash content; NDSF, neutral detergent soluble fibre; n/a, unselected variables in the model

	Lodgepole pine		Sagebrush		Combined	
	HC	LFMC	HC	LFMC	HC	LFMC
R^2_{adj}	0.55	0.84	0.90	0.96	0.77	0.61
RMSE	0.35	10.79	0.13	7.66	0.33	19.75
NDF	−0.01	0.84	n/a	n/a	n/a	0.92
NSC	0.02	−2.44	0.07	−5.96	0.04	−3.17
CP	n/a	6.55	n/a	12.33	n/a	n/a
CF	0.11	−4.03	0.05	−5.22	0.06	−5.03
AC	n/a	n/a	−0.28	14.75	−0.27	4.81
NDSF	n/a	n/a	n/a	2.5	n/a	n/a
Intercept	20.8	100.87	20.1	−18.84	20.7	141.02

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