Decoupling seasonal changes in water content and dry weight to predict live conifer foliar moisture content

W. Matt Jolly[1,2], Ann M. Hadlow[1] and Kathleen Huguet[1]

[1]US Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, 5775 Hwy 10 W, Missoula, MT, USA 59808

[2]Corresponding Author:

Email: mjolly@fs.fed.us
Tel: +01 406 360 7356
Fax: +01 406 329 4825

Abstract

Live foliar moisture content (LFMC) significantly influence the ignition and spread of wildland fires. However, characterizing seasonal changes in LFMC is difficult because both foliar water content and dry matter can change throughout the season. Here we present the results of a study aimed at quantifying the seasonal changes in both plant water status and dry matter partitioning. We collected new and old foliar samples from *Pinus contorta* for two growing seasons and we quantified their foliar moisture content, relative water content and dry matter chemical partitioning. We found that the amount of starches, sugars and crude fats in the foliage explained more of the seasonal variations in LFMC than relative water content. We show that a combination of relative water content, non-structural carbohydrates, crude fat and ash content can explain 92% of the variation in live foliar moisture content throughout the entire study period. These results suggest that models attempting to characterize seasonal variations in LFMC must separately consider seasonal changes in actual water content and dry matter partitioning. We suggest that a physiological modeling approach to assessing live foliar moisture content dynamics is needed over approaches that simply attempt to correlate LFMC to indicators of drought stress alone.

Keywords: foliar moisture content, relative water content, carbohydrates, crude fat, dry matter, model

1 Introduction

Wildland fires are common global ecosystem disturbances (Bowman et al. 2009) and these fires spread through a combination of living and dead vegetation. Many environmental factors influences how these fires behave but fuel moisture content (FMC) has long been shown to influence how wildland fires ignite and spread (Gisborne 1936, Fons 1946, Anderson and Rothermel 1965, Xanthopoulos and Wakimoto 1993, Dimitrakopoulos and Papaioannou 2001, Weise et al. 2005, Pellizzaro et al. 2007b). Fuel moisture can affect the preheating of fuels (Byram 1959) and the resulting water vapor can attenuate radiant heat transfer to adjacent fuels (Frankman et al. 2008). As such, fires spread faster through fuels with lower moisture contents (Anderson and Rothermel 1965).

Fuel moisture content expresses the ratio of the mass of the water contained in a sample to the dry mass of the sample. This metric can be applied to any vegetation component, such as stems, branches and foliage as well as for living or dead vegetation. In its simplest form, fuel moisture content can be expressed as follows:

$$\text{Fuel Moisture Content (FMC)} = \text{Water Mass} / \text{Dry Mass} \qquad \textbf{Equation 1}$$

While both live and dead fuel moisture content are important factors in fire behavior, the mechanisms that drive their spatial and temporal variations are different (Nelson Jr. 2001). Dead fuel moisture contents are generally driven by direct diffusion of water into and out of the fuel (Viney 1991, Nelson 2000). Their calculated moisture content can only change as a function of changes in the fuel’s water weight because their dry matter changes very little over a season and would only decline as a function of long-term decomposition. In contrast, live fuel moisture content, particularly that of foliage, can vary either due to changes in its actual water content or through possible changes in its dry weight and thus is driven more by plant physiological processes such as phenology, soil water uptake, evapotranspiration and photosynthesis (Kozlowski and Pallardy 1979). Ackely (1954) suggested that changes in Bartlett pear foliar moisture content were more linked to changes in dry matter than to changes in actual water content. Additionally, Little (1970) demonstrated that seasonal changes in carbohydrates and fats explain some of the observed seasonal changes in moisture content but they suggest that concurrent changes in water content must also be important. Others have suggested that the moisture dynamics of live foliage are a combination of seasonal changes in actual water content and dry matter change (Kozlowski and Clausen 1965, Gary 1971). Ultimately, these previous studies underscore the need for a more complete understanding of the factors that drive seasonal changes in live foliar moisture content to better enable us to interpret measured seasonal changes and to develop more robust models to assess their seasonality.

Here we present the results of a study aimed at linking seasonal changes in live foliar moisture content to seasonal changes in both foliar chemistry and actual water content. We sample foliage from a common Intermountain US conifer for two seasons and we determine its chemical make-up, foliar moisture content and actual water content. We then evaluate the relationships between foliar moisture content, foliar water content and chemistry and we attempt to elucidate the elements that best explain seasonal variations in live foliar moisture content.

2 Materials and Methods

2.1 Sample Sites

Foliar samples were collected from *Pinus contorta* trees at two proximal sites located on an exposed South or Southwest aspect in Western Montana, USA. The first site (Lubrecht) was at 1262 meters (4141 ft) elevation and was located on the Lubrecht Experimental Forest (46.89785° Lat., -113.4395° Long.). The second site (Garnet) was at 1699 meters (5575 ft) elevation and was located on the Garnet Range Road (46.85183° Lat., -113.4036° Long.).

2.2 Foliar Moisture Content

Foliar samples were collected weekly from May through October 2010 and July through August 2011. They were taken from branches at the lower 1/3 of trees growing in road cuts. Sampling only from exposed crowns helped to control for within-crown foliar moisture content differences that are observed due to shading (Pook and Gill 1993). Current year foliage was collected separate from previous year's foliage because there are generally large differences between old and new foliar moisture content until the new foliage is fully matured (Chrosciewicz 1986). Old growth was sampled irrespective of needle age class but was generally less than six years old. All samples were kept cool after collection and all laboratory measurements were made on the day of collection, usually within two hours.

Three, two gram samples of needles from each needle age class (new or old) and site were collected for each sampling date. Samples were weighed as soon as possible after collection to obtain their fresh (wet) weight using a scale accurate to the nearest 10 mg. Samples were weighed with lids on to prevent moisture. Samples were dried with lids off in a 95°C forced air convection oven for 48 hours. Cans were reweighed after drying to determine dry weight. Can weights were also recorded and foliar moisture content was calculated using the following equation that removes the tare weight of the sample cans:

$$\mathbf{LFMC = ((FW\text{-}DW) / (DW - TareW)) \times 100} \qquad \textbf{Equation 2}$$

Where FMC is the live foliar moisture content, FW is the sample Fresh Weight (g), DW is the sample Dry Weight (g), and TareW is the weight of the empty sample cans and lids. This equation is convenient for field sampling because it does not require the subtraction of the tare weights from each component of the calculation but it is mathematically equivalent to doing so. Foliar moisture content was used to calculate the water mass and dry mass on a fresh weight basis using the following equation:

$$DM = 1 / ((LFMC/100)+1) \qquad \textbf{Equation 3}$$

$$WM = 1 - DM \qquad \textbf{Equation 4}$$

Where DM (g) is the dry matter for a one kilogram of fresh fuel and WM (kg) is the mass of water contained in one kilogram of fresh fuel.

2.3 Relative Water Content

Relative Water Content (RWC) is a standard metric used by physiologists to quantify the water status of plants (Barrs and Weatherley 1962). RWC was measured by taking three, one gram samples of needles and first measuring their fresh weight. Samples were then soaked for 24 hours in distilled water, blotted dry and re-weighed for their turgid weight. Samples were then dried for 48 hours at 95°C in a forced air convection oven. Relative water content was then calculated as follows:

$$\mathbf{RWC = ((FW\text{-}DW) / (TW - DW)) \times 100} \qquad \textbf{Equation 5}$$

Where RWC is the Relative Water Content (% turgid wt), FW is the sample Fresh Weight (g), DW is the sample dry weight (g) and TW is the samples turgid weight (g) determined after the 24 hour rehydration period. This value expresses the moisture content of the sample as a fraction of its saturated weight and it is naturally bounded between 0 and 100.

2.4 Foliar chemistry

Each week, a twenty gram sub-sample was collected from the same foliar samples used to determine foliar moisture content and relative water content. New and old foliage were separated when both were present. Leaf chemical composition was determined using the wet reference method by an external forage testing laboratory (AOAC 1984, Horwitz and Latimer 2000, AgriAnalysis 2012). The analysis provided measurements of neutral detergent fiber (Fiber carbohydrates) (NDF), Non-fiber carbohydrates (NFC), crude fat (CF), crude protein (CP) and ash content (AC). Additional measurements of total non-structural carbohydrates (NSC) were also made. These measurements provided estimates of total starch and total sugar. Crude protein was determined using a TruSpec combustion analyzer. Crude fat was determined using an ANKOM Fat Analyzer with petroleum ether. NDF was determined using an ANKOM 200 Fiber Analyzer. Non-fiber carbohydrates (NFC) were calculated by the difference method using the following equation:

$$\mathbf{NFC = 100 - NDF + CF + CP + AC} \qquad \textbf{Equation 6}$$

Neutral detergent fiber quantifies the structural carbohydrates such as cellulose, hemicellulose and lignin, while non-fiber carbohydrates are generally water soluble and represent primarily sugars, starches, and other non-structural carbon compounds in the leaves. 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 foliage and ash content quantifies the mineral content of the needle.

2.5 Data Analysis

All data analysis was performed using the R statistical software package, version 2.15.5. Foliar moisture content was compared to relative water content and the six foliar chemistry variables using Pearson's correlations. Where appropriate, variables were log-transformed to provide a more linear relationship between variables. The best-fit model for predicting live foliar moisture content as a function of relative water content and chemistry was determined using a stepwise, ordinary least squares regression.

3 Results

Seasonal mean and standard deviations for foliar moisture content, relative water content and six foliage chemistry groups are shown in Table 1. Average seasonal moisture content, relative water content, fiber carbohydrates and protein were higher in new foliage than in old foliage. In contrast, old foliage had higher percentages of non-fiber carbohydrates, including starch and sugar, and crude fat. Seasonal plots of these variables are also shown in Figure 1. Strong seasonal declines in foliar moisture content were noted for new needles at both sites. These changes were concurrent with a slight increase in foliar moisture content of old needles at both sites. In contrast, no strong seasonal decline was noted in relative water contents but RWC did show seasonal minimums during late summer when water stress would likely have been highest (Figure 1B). New needles were composed of proportionally more fiber carbohydrates as compared to old needles but had relatively consistent percentages of non-fiber carbohydrates across both new and old needles for both sites. Sugar and starch content of new needles doubled over the growing season and crude fat content of new needles tripled. Protein and ash content was little changed throughout the season.

It was noted that the relationships between foliar moisture content and the other variables was non-linear. Therefore, for further analysis, all variables were log-transformed. Correlations between these log-transformed independent variables and live foliar moisture content were given in Table 2 and these relationships are also plotted in Figure 2. Foliar moisture content was found to be strongly related to dry weight percentages of non-structural carbohydrates (sugar and starch) and crude fat ($\rho = -0.915$ and -0.937, respectively). FMC was moderately correlated with relative water content ($\rho = 0.71$).

The results of the step-wise, ordinary least squares regression are given in Table 3. Relative water content, non-structural carbohydrates, crude fat and ash were selected as the variables that best explained the variations in foliar moisture content. These variables explained 92% of the variation in live foliar moisture content. The fitted model was then used to predict foliar moisture content and these predictions are shown graphically as compared to the measured foliar moisture content in Figure 1. The coefficient for relative water content and ash was positive, indicating that as these values increase, foliar moisture content increases. In contrast, the coefficients for non-structural carbohydrates and crude fat were negative, indicating that as these variables increase, foliar moisture content decreased.

Table 1 – Seasonal mean and stand deviations of moisture content, relative water content and foliar chemistry for Lodgepole pine foliage.

	New Needles (Lubrecht)	New Needles (Garnet)	Old Needles (Lubrecht)	Old Needles (Garnet)
Foliar Moisture Content (% dry wt)	178.6 (39.4)	180.7 (42.7)	105.2 (11.3)	105.6 (9.0)
Relative Water Content (% turgid wt)	84.9 (2.5)	83.8 (3.9)	74.8 (2.9)	77.1 (3.8)
Fiber Carbohydrates (% dry wt)	44.6 (4.3)	45.8 (4.4)	39.9 (3.0)	41.1 (3.1)
Non-fiber Carbohydrates (% dry wt)	41.9 (4.1)	40.1 (4.2)	42.0 (3.2)	41.3 (3.4)
Starch / Sugar (% dry wt)	9.4 (2.7)	8.3 (2.6)	17.8 (2.3)	16.1 (2.2)
Crude Fat (% dry wt)	3.5 (1.0)	3.7 (1.2)	8.6 (0.6)	7.6 (0.8)
Protein (% dry wt)	8.0 (0.5)	8.3 (0.8)	7.2 (0.5)	7.7 (0.6)
Ash (% dry wt)	1.9 (0.2)	2.0 (0.3)	2.4 (0.3)	2.3 (0.5)

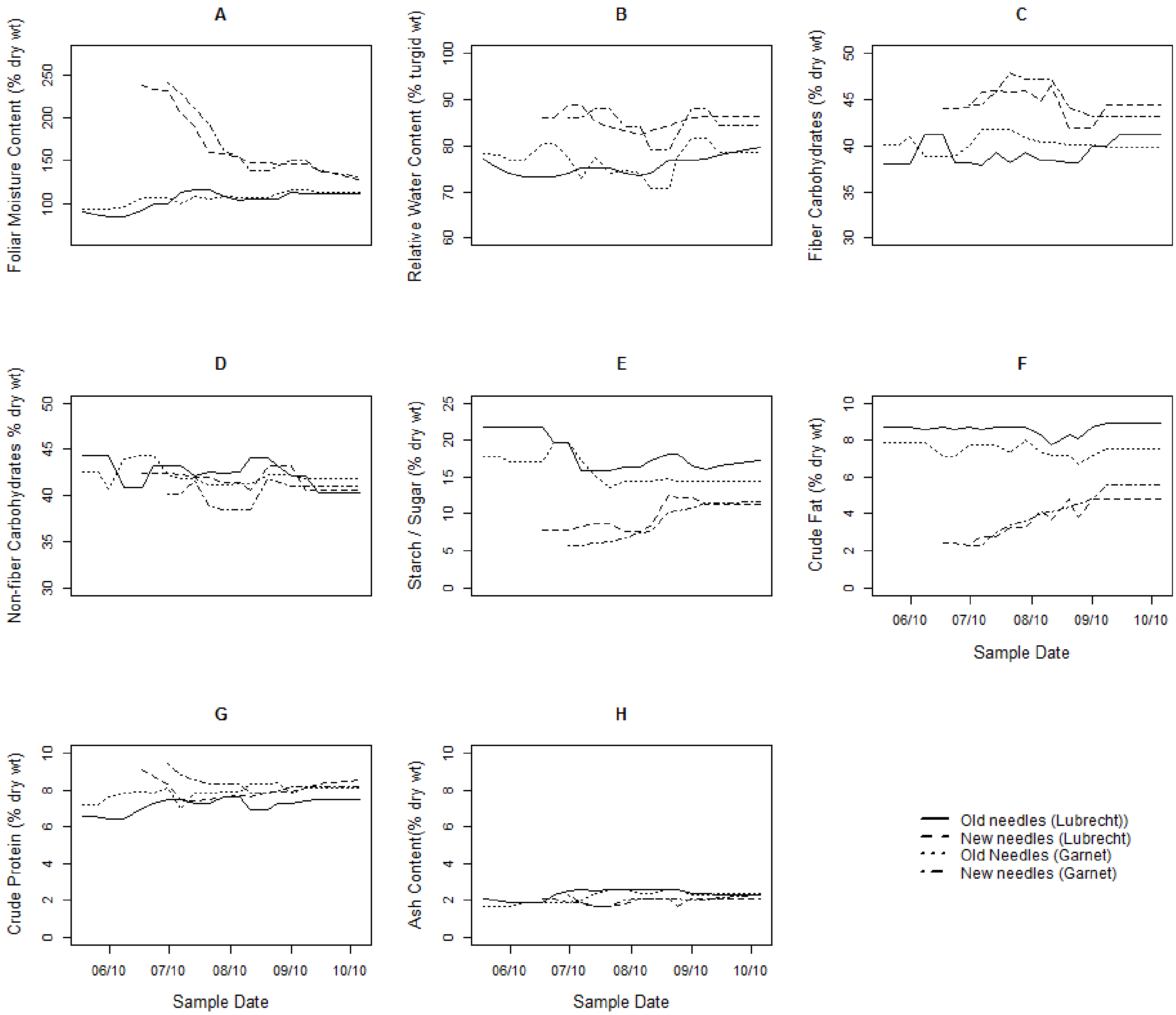

Figure 1 – Seasonal variations in foliar moisture content, relative water content and four chemical component of Lodgepole pine foliage from May – October 2010. Strong declines in the foliar moisture content (A) of new needles at both sites correspond to increases in the starch and sugar content (E) and crude fat of the foliage (F). New needles were composed of a higher percentage of fiber carbohydrates (C) but had approximately the same non-fiber carbohydrate percentage as old needles (D). Crude protein declined slight in new needles during the early part of the growing season but eventually matched that of old needles by August. Ash content (H) showed little variation between old and new needles for both sites.

Table 2 – Correlations between live foliar moisture content and various leaf chemistry and moisture metrics. Live foliar moisture content was strongly related to changes in non-structural carbohydrates and crude fats and moderately related to changes in relative water content.

Variable	**Correlation with log(live foliar moisture content) (N=77)**
Log(Relative Water Content (% turgid wt))	**0.710 *** **
Log(Fiber Carbohydrates (NDF) (% dry wt))	**0.550 *** **
Log(Non-fiber Carbohydrates (NFC) (% dry wt))	**-0.139 (NS)**
Log(Non-structural Carbohydrates (NSC) (% dry wt))	**-0.915 *** **
Log(Crude Protein (% dry wt))	**0.642 *** **
Log(Crude Fat (% dry wt))	**-0.937 *** **
Log(Ash Content (% dry wt))	**-0.322 ** **

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

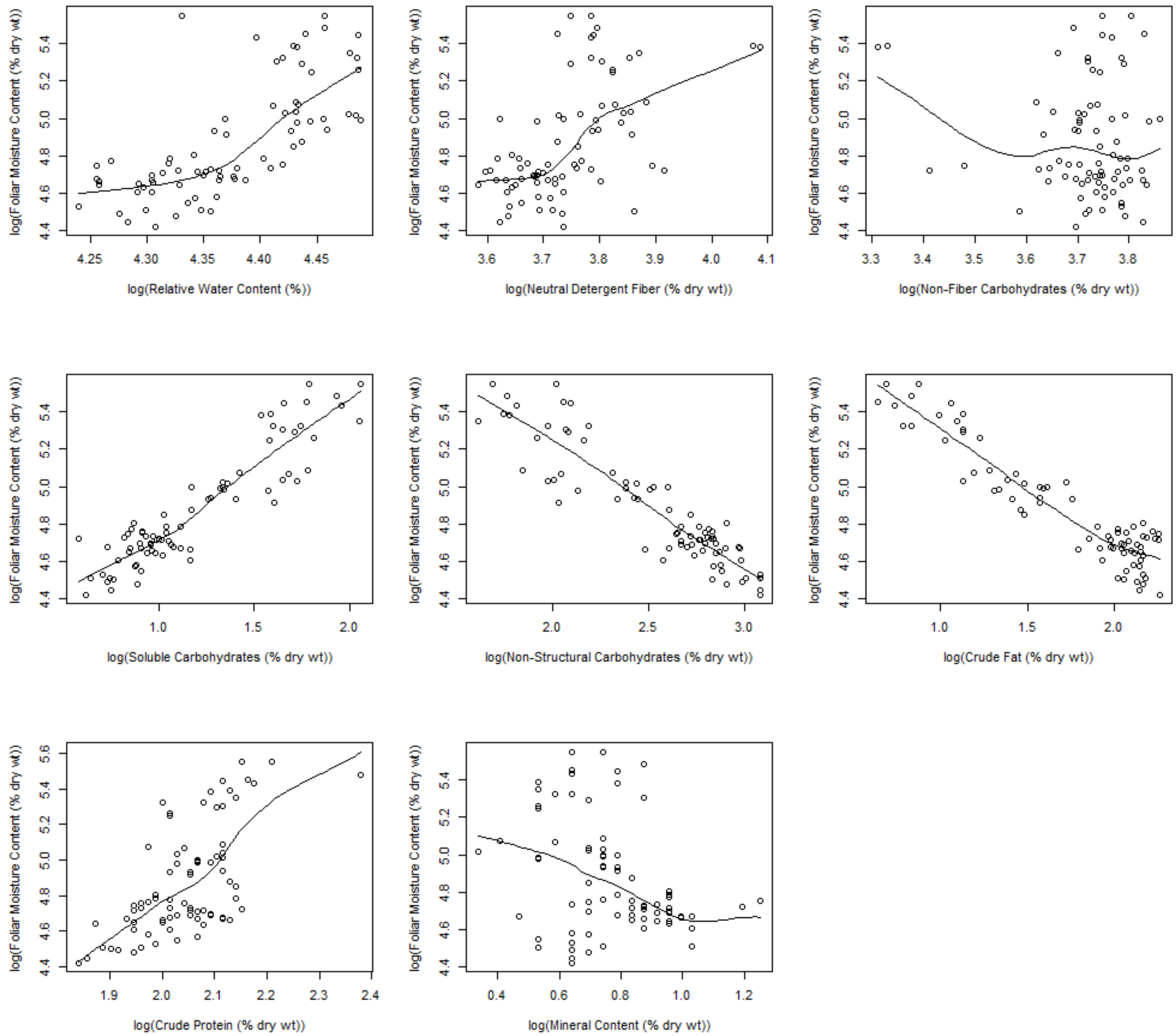

Figure 2 – Relationships between foliar moisture content, relative water content and the six chemical constituents of foliage. The relationship between foliar moisture content and these variables was more linear when the variables were log-transformed. Plots are shown with a locally-estimated smoothing spline (LOESS) for reference.

Table 3 – Results of the stepwise, ordinary least squares regression model fit predicting foliar moisture content as a function of relative water content and foliar chemistry. Relative water content, non-structural carbohydrates, crude fat and ash content were selected as the best predictors of live foliar moisture content.

	Coefficient	**Intercept**	**F-Statistic**	**R^2**
Log(Relative Water Content)	0.47955*	3.92925 ***	200.8 ***	0.9177
Log(Non-structural Carbohydrates)	-0.24733***			
Log(Crude Fat)	-0.38421***			
Log(Ash Content)	0.17084*			

* $p < 0.05$

** $p < 0.001$

*** $p < 0.001$

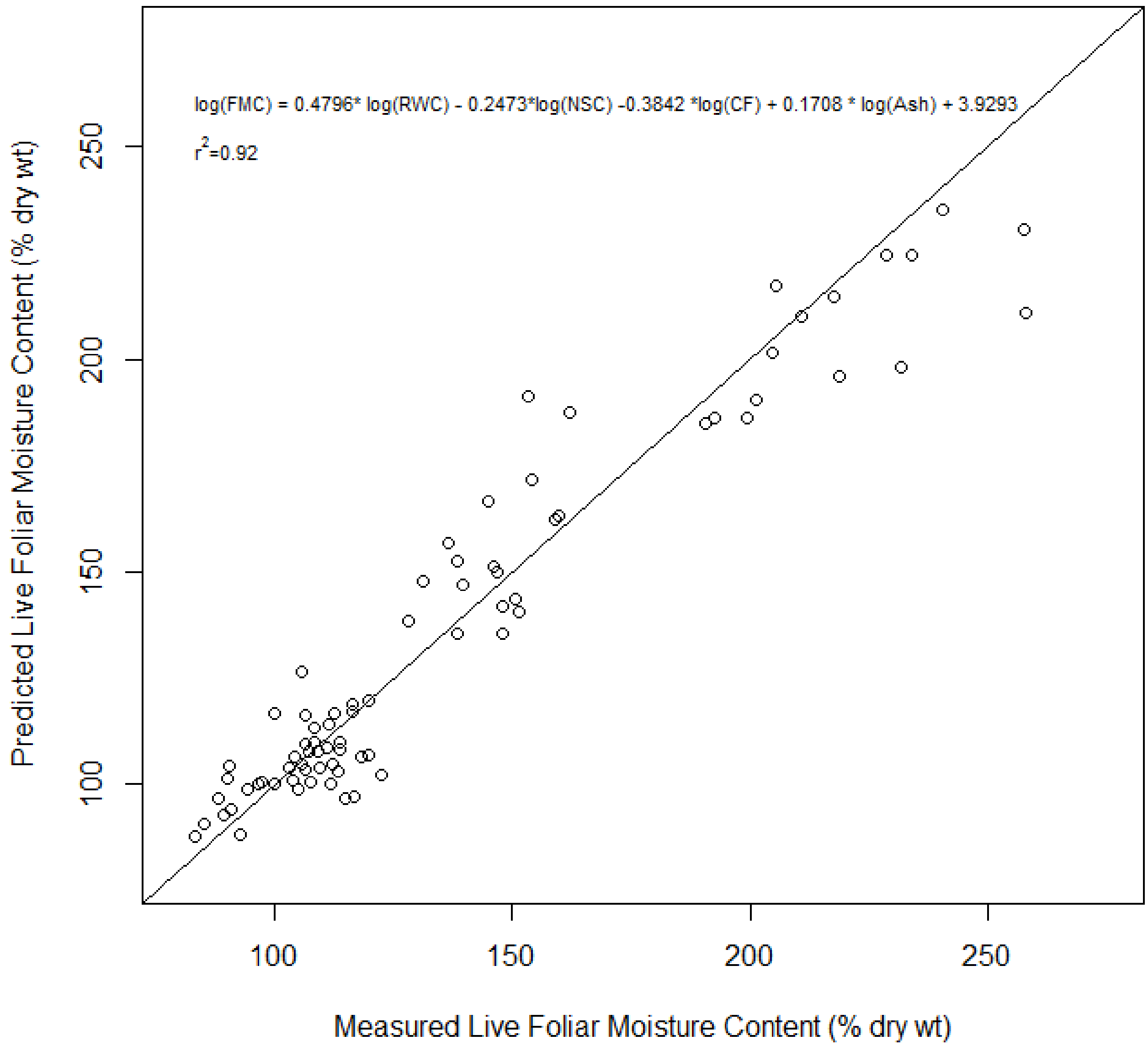

Figure 3 – Measured versus predicted live foliar moisture content for Lodgepole pine foliage. Foliar moisture content was best predicted as a function of Relative Water Content (RWC), Non-structural Carbohydrates (NSC), Crude Fat (CF) and Ash content (OLS, $p < 0.001$, $F = 200.8$, $r2 = 0.92$, $n=77$).

4 Discussion

Live foliar moisture content has long been recognized as an important determinant of the flammability of vegetation. Consequently, it is necessary to completely understand the factors that drive the variations in LFMC in order to assess spatial and temporal changes in the potential for the start and spread of wildland fires through live fuels. Our results underscore the importance of seasonal foliar dry weight changes and stress the need to evaluate changes in measured moisture within the context of both changes in the actual water content of the foliage as well as changes in the dry weight of the foliage. Additionally, it emphasizes the need to completely understand the linkages between the carbon and water cycles of plants in order to truly understand live fuel moisture dynamics.

Previous work has attempted to link the seasonal dynamics of live foliar moisture content to changes in meteorological conditions, such as those that are depicted by various drought indices (Viegas et al. 2001, Castro et al. 2003, Dennison et al. 2003, Dimitrakopoulos and Bemmerzouk 2003, Pellizzaro et al. 2007a). However, these studies have met with limited or mixed success. For example, for some Mediterranean shrub species, Pellizario et. al. (2007a) found strong correlations between live foliar moisture content and five drought indices during periods of water stress but poor correlations as drought stress was relieved. Also, Dimitrakopoulos and Bemmerzouk (2003) found that while drought indices closely match the moisture content of herbaceous plants, they were poorly correlated with the foliar moisture content of deep-rooted *Pinus brutia* trees. De-coupling the effects of water stress from seasonal dry matter changes would have likely strengthened these studies.

Intuitively, live foliar moisture content can be divided into two separate, yet complimentary components as expressed in Equation 1. The changes in the absolute mass of the water (numerator of Equation 1) should be most related to the water cycle of the trees and can be directly linked to the Soil-Vegetation-Atmosphere continuum (Nelson Jr. 2001). It is regulated by all the factors that dictate the rate of uptake of water from the soil, transport to the leaves and loss through the foliar stomata. The second component is the dry matter change (denominator of Equation 1). These dynamics are most related to the phenology of the plant which dictates the timing of new foliar growth and their rates of development. Dry matter changes are also related to carbon uptake and translocation through photosynthesis as evidenced by the strong relationships that we found between non-structural carbohydrates and foliar moisture content. Ultimately, attempts to better understand the dynamics of live fuel moisture must consider both water weight and dry weight changes and their driving factors to adequately describe these seasonal changes.

Our results show that the moisture contents of new and old needles are significantly different throughout most of the growing season. However, often these two foliar components are not separated at sampling and they may be combined into a single sample during collection (eg. (Castro et al. 2003, Pellizzaro et al. 2007a). This sampling strategy would explain why seasonal live fuel moisture values typically show a rise to some peak value and an eventual decline. Much of these dynamics can be explained by the mixing of new foliage with a high moisture content, with old foliage with a lower moisture content. Others have suggested the need to separate new and old foliage when sampling and they have demonstrated the large discrepancies in moisture content between these two foliar categories (Chrosciewicz 1986, Agee et al. 2002).

Our results extend these studies by showing the large differences in dry matter composition between old and new needles and it emphasizes the need to separate new and old foliage when sampling live foliar moisture content. Additionally, it emphasizes the need to develop a better understanding of canopy development, such as the timing and rate needle elongation and needle hardening, to better assess canopy-scale foliar moisture content.

Changes in dry matter are likely a dynamic combination of foliar development, photosynthesis, respiration and carbon allocation. During the early period of develop, we saw large declines in old needle foliar moisture content and slight increases in the moisture content of new needles. These changes were observed concurrent with continuous increases in the non-structural carbohydrates and crude fats of new needles and slight declines of those chemical components in new needles. These changes are likely a function of the complex linkages between growth and respiration of new needles.   During early needle development, carbon is translocated from old needles to new needles (Gordon and Larson 1968). This causes the dry weight of old needles to decrease (and their apparent foliar moisture content to increase) and the dry weight of the new needles increases (and their apparent foliar moisture content decreases).   New needles also have a high demand for carbohydrates during their early development and they only export carbon to other parts of plant several weeks after they are fully developed (Ericsson 1978). Thus, it is important to understand the physiological drivers that control the dry matter changes in live fuels if we are to be better able to predict their seasonal dynamics.

Considerable interest has also been paid to the remote estimation of live foliar moisture content using various satellite indices (Chuvieco et al. 2004, Danson and Bowyer 2004, Dennison et al.

2005, Dasgupta et al. 2007, Hao and Qu 2007, Yebra et al. 2008). Ground-based spectra measurements have shown that live foliar moisture content relates well to both metrics that quantify the vegetation's photosynthetic capacity as well as their water content (Piñol et al. 1998). Others have shown that the actual plant reflectance at the canopy scale is sensitive to be water content and plant dry matter differences (Bowyer and Danson 2004). Thus a better understanding of the individual dynamics of plant water status and foliar dry matter may help improve our ability to more adequately assess live foliar moisture content by remote sensing.

Ultimately, our results suggest that while studies have shown linkages between live foliar moisture content and meteorological conditions, the causes of the actual changes in measured moisture content are more complex. Future work must focus on decoupling the factors that drive seasonal changes in water content and dry matter composition to better assess the causes for seasonal variations in live foliar moisture content.

5 Acknowledgements

This work was completed in part by a grant from the Joint Fire Science Program (Grant No. JFSP- 10-1-08-6). We would like to thank the Lubrecht Experimental Forest of The University of Montana, College of Forestry and Conservation, and the Department of the Interior, Bureau of Land Management for providing access for foliar sampling.

6 References

Ackley, W. B. 1954. Seasonal and diurnal changes in the water contents and water deficits of Bartlett pear leaves. Plant Physiology **29**:445.

Agee, J. K., C. S. Wright, N. Williamson, and M. H. Huff. 2002. Foliar moisture content of Pacific Northwest vegetation and its relation to wildland fire behavior. Forest Ecology and Management **167**:57-66.

AgriAnalysis. 2012. Forage Analysis Laboratory.

Anderson, H. E. and R. C. Rothermel. 1965. Influence of moisture and wind upon the characteristics of free-burning fires. Symposium (International) on Combustion **10**:1009-1019.

AOAC. 1984. Official methods of analysis. Association of Official Analytical Chemists: Washington, DC **43**:7.009.

Barrs, H. D. and P. E. Weatherley. 1962. A re-examination of the relative turgidity technique for estimating water deficits in leaves. Australian Journal of Biological Sciences **15**:413-428.

Bowman, D. M. J. S., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. Dâ€™Antonio, R. S. DeFries, J. C. Doyle, S. P. Harrison, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, J. B. Marston, M. A. Moritz, I. C. Prentice, C. I. Roos, A. C. Scott, T. W. Swetnam, G. R. van der Werf, and S. J. Pyne. 2009. Fire in the Earth System. Science **324**:481-484.

Bowyer, P. and F. M. Danson. 2004. Sensitivity of spectral reflectance to variation in live fuel moisture content at leaf and canopy level. Remote Sensing of Environment **92**:297-308.

Byram, G. M. 1959. Combustion of Forest Fuels.*in* K. P. Davis, G. M. Byram, and W. R. Krumm, editors. Forest Fire: Control and Use. McGraw-Hill Book Company, New York, NY.

Castro, F. X., A. Tudela, and M. T. SebastiÄ…. 2003. Modeling moisture content in shrubs to predict fire risk in Catalonia (Spain). Agricultural and forest meteorology **116**:49-59.

Chrosciewicz, Z. 1986. Foliar moisture content variations in four coniferous tree species of central Alberta. Canadian Journal of Forest Research **16**:157-162.

Chuvieco, E., D. Cocero, D. Riano, P. Martin, J. MartÃ±nez-Vega, J. De La Riva, and F. PÃ©rez. 2004. Combining NDVI and surface temperature for the estimation of live fuel moisture content in forest fire danger rating. Remote Sensing of Environment **92**:322-331.

Danson, F. M. and P. Bowyer. 2004. Estimating live fuel moisture content from remotely sensed reflectance. Remote Sensing of Environment **92**:309-321.

Dasgupta, S., J. J. Qu, X. Hao, and S. Bhoi. 2007. Evaluating remotely sensed live fuel moisture estimations for fire behavior predictions in Georgia, USA. Remote Sensing of Environment **108**:138-150.

Dennison, P. E., D. A. Roberts, S. H. Peterson, and J. Rechel. 2005. Use of Normalized Difference Water Index for monitoring live fuel moisture. International Journal of Remote Sensing **26**:1035-1042.

Dennison, P. E., D. A. Roberts, S. R. Thorgusen, J. C. Regelbrugge, D. Weise, and C. Lee. 2003. Modeling seasonal changes in live fuel moisture and equivalent water thickness using a cumulative water balance index. Remote Sensing of Environment **88**:442-452.

Dimitrakopoulos, A. P. and A. M. Bemmerzouk. 2003. Predicting live herbaceous moisture content from a seasonal drought index. International Journal of Biometeorology **47**:73-79.

Dimitrakopoulos, A. P. and K. K. Papaioannou. 2001. Flammability Assessment of Mediterranean Forest Fuels. Fire Technology **37**:143-152.

Ericsson, A. 1978. Seasonal Changes in Translocation of 14C from Different Age-Classes of Needles on 20-Year-Old Scots Pine Trees (Pinus silvestris). Physiologia Plantarum **43**:351-358.

Fons, W. L. 1946. Analysis of fire spread in light forest fuels. Journal of Agricultural Research **72**:93-121.

Frankman, D., B. W. Webb, and B. W. Butler. 2008. Influence of absorption by environmental water vapor on radiation transfer in wildland fires. Combustion Science and Technology **180**:509-518.

Gary, H. L. 1971. Seasonal and diurnal changes in moisture contents and water deficits of Engelmann spruce needles. Botanical Gazette:327-332.

Gisborne, H. T. 1936. Measuring fire weather and forest inflammability. US Dept. of Agriculture.

Gordon, J. C. and P. R. Larson. 1968. Seasonal course of photosynthesis, respiration, and distribution of C14 in young Pinus resinosa trees as related to wood formation. Plant Physiology **43**:1617-1624.

Hao, X. and J. J. Qu. 2007. Retrieval of real-time live fuel moisture content using MODIS measurements. Remote Sensing of Environment **108**:130-137.

Horwitz, W. and G. W. Latimer. 2000. Official methods of analysis of AOAC International. AOAC international Gaithersburg, MD.

Kozlowski, T. T. and J. J. Clausen. 1965. Changes in Moisture Contents and Dry Weights of Buds and Leaves of Forest Trees. Botanical Gazette **126**:20-26.

Kozlowski, T. T. and S. G. Pallardy. 1979. The physiology of woody plants. Academic Press, San Diego.

Little, C. H. A. 1970. Seasonal changes in carbohydrate and moisture content in needles of balsam fire (Abies balsamea). Canadian Journal of Botany **48**:2021-2028.

Nelson Jr., R. M. 2001. Water relations of forest fuels.*in* E. A. Johnson and K. Miyanishi, editors. Forest fires: Behavior and Ecological Effects. Academic Press, London, UK.

Nelson, R. M. 2000. Prediction of diurnal change in 10-h fuel stick moisture content. Canadian Journal of Forest Research **30**:1071-1087.

Pellizzaro, G., C. Cesaraccio, P. Duce, A. Ventura, and P. Zara. 2007a. Relationships between seasonal patterns of live fuel moisture and meteorological drought indices for Mediterranean shrubland species. International Journal of Wildland Fire **16**:232-241.

Pellizzaro, G., P. Duce, A. Ventura, and P. Zara. 2007b. Seasonal variations of live moisture content and ignitability in shrubs of the Mediterranean Basin. International Journal of Wildland Fire **16**:633-641.

Piñol, J., I. Filella, R. Ogaya, and J. Peñuelas. 1998. Ground-based spectroradiometric estimation of live fine fuel moisture of Mediterranean plants. Agricultural and forest meteorology **90**:173-186.

Pook, E. W. and A. M. Gill. 1993. Variation of Live and Dead Fine Fuel Moisture in *Pinus radiata* Plantations of the Australian-Capital-Territory. International Journal of Wildland Fire **3**:155-168.

Viegas, D. X., J. Piñol, and R. Ogaya. 2001. Estimating live fine fuels moisture content using meteorologically-based indices. International Journal of Wildland Fire **10**:223-240.

Viney, N. R. 1991. A review of fine fuel moisture modelling. International Journal of Wildland Fire **1**:215-234.

Weise, D. R., X. Zhou, L. Sun, and S. Mahalingam. 2005. Fire spread in chaparral - 'go or no-go?'. International Journal of Wildland Fire **14**:99-106.

Xanthopoulos, G. and R. H. Wakimoto. 1993. A time to ignition - temperature - moisture relationship for branches of three western conifers. Canadian Journal of Forest Research **23**:253-258.

Yebra, M., E. Chuvieco, and D. RiaÃ±o. 2008. Estimation of live fuel moisture content from MODIS images for fire risk assessment. Agricultural and forest meteorology **148**:523-536.