

# De-coupling seasonal changes in water content and dry matter to predict live conifer foliar moisture content

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**Abstract.** Live foliar moisture content (LFMC) significantly influences wildland fire behaviour. However, characterising variations in LFMC is difficult because both foliar mass and dry mass can change throughout the season. Here we quantify 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 quantified their LFMC, relative water content (RWC) and dry matter chemistry. LFMC quantifies the amount of water per unit fuel dry weight whereas RWC quantifies the amount of water in the fuel relative to how much water the fuel can hold at saturation. RWC is generally a better indicator of water stress than is LFMC. We separated water mass from dry mass for each sample and we attempted to best explain the seasonal variations in each using our measured physiochemical variables. We found that RWC explained 59% of variation in foliar water mass. Additionally, foliar starch, sugar and crude fat content explained 87% of the variation in seasonal dry mass changes. These two models combined explained 85% of the seasonal variations in LFMC. These results demonstrate that changes to dry matter exert a stronger control on seasonal LFMC dynamics than actual changes in water content, and they challenge the assumption that LFMC variations are strongly related to water stress. This methodology could be applied across a range of plant functional types to better understand the factors that drive seasonal changes in LFMC and live fuel flammability.

**Additional keywords:** carbohydrates, crude fat, model, relative water content.

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## Introduction

Wildland fires are a common global ecosystem disturbance (Bowman *et al.* 2009) and they spread through a combination of living and dead vegetation. Many environmental factors influence 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; Van Wilgen *et al.* 1985; Cruz *et al.* 2005; Davies *et al.* 2009). Fuel moisture can affect the preheating of fuels (Byram 1959), and the resulting water vapour can attenuate radiant heat transfer to adjacent fuels (Frankman *et al.* 2008), causing fires to spread faster through fuels with lower moisture contents (Anderson and Rothermel 1965).

FMC 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 to living or dead vegetation. In its simplest form, FMC can be expressed as follows:

$$\text{FMC} = \text{water mass} \div \text{dry mass} \quad (1)$$

Although both live and dead FMC are important factors in fire behaviour, the mechanisms that drive their spatial and temporal variations are different (Nelson 2001). Dead fuel

moisture content (DFMC) is generally driven by direct diffusion of water into and out of the fuel (Viney 1991; Nelson 2000). DFMC is driven by the weather conditions around the fuel and only changes as a function of changes in the fuel's water weight, because dry matter remains constant. In contrast, live fuel moisture content (LFMC), particularly of foliage, is driven more by plant physiological process, varying from changes in its water content due to soil water uptake and evapotranspiration, or through possible changes in its dry mass due to phenology and photosynthesis (Kozlowski and Pallardy 1979). Ackley (1954) suggested that changes in Bartlett pear (a *Pyrus communis* cultivar) FMC 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 FMC but they suggest that concurrent changes in water content must also be important. Others have suggested that the dynamics of LFMC are a combination of seasonal changes in actual water content and dry matter change (Kozlowski and Clausen 1965; Gary 1971). More work is needed to understand the factors that drive seasonal changes in LFMC and enable us to develop more robust models to assess and interpret its seasonality.

LFMC is a parameter in many empirical and physical fire behaviour models (Rothermel 1972; Van Wagner 1977; Linn

*et al.* 2002; Mell *et al.* 2007) and there is considerable effort to periodically measure LFMC as an indicator of wildland fire potential (Brenner 2002; Stonex *et al.* 2004). However, relationships between LFMC and fire behaviour are still poorly understood. A recent review by Alexander and Cruz (2013) suggests that LFMC may not significantly influence live crown fire spread rates despite the many studies that have demonstrated linkages between LFMC and flammability in both field experiments and laboratory burns (Van Wilgen *et al.* 1985; Xanthopoulos and Wakimoto 1993; Dimitrakopoulos and Papaioannou 2001; Cruz *et al.* 2005; Weise *et al.* 2005; Pellizzaro *et al.* 2007a). One reason for these inconsistencies may be that physical descriptions of live fuel dynamics that include both water and dry matter partitioning are lacking. This may be important because both water content and chemical composition are important factors in fuel flammability (Finney *et al.* 2013). Ultimately, describing the interactions between seasonal changes in water mass, dry mass and subsequent LFMC may improve our ability to assess how living plants influence wildland fire behaviour.

Here we present a study aimed at linking seasonal changes in LFMC to seasonal changes in both foliar water mass and dry mass. We sampled foliage from a common conifer of the United States Intermountain region for two seasons and determined its chemical make-up, plant water status and LFMC. We then decomposed FMC into its respective water mass and dry mass proportions. Finally, we developed linear models to separately predict water mass and dry mass based on their respective relationships with plant water status and foliar chemistry, and we combine these two linear models to predict seasonal variation in LFMC.

## Materials and methods

### Sample sites

Foliar samples were collected from *Pinus contorta* (lodgepole pine) trees at two proximal sites located on exposed south or south-west aspects in Western Montana, USA. The Lubrecht site was at an elevation of 1262 m (4141 ft) and was located on the Lubrecht Experimental Forest (46°53'52.3"N, 113°26'22.2"W). The Garnet site was at an elevation of 1699 m (5575 ft) and was located on the Garnet Range Road (46°51'06.6"N, 113°24'13.0"W).

### Foliar moisture content

Foliar samples were collected weekly from May to October 2010 and July to August 2011. They were taken from branches at the lower third of trees growing in road cuts. Sampling only from exposed crowns helped to control for within-crown foliar moisture content differences known to occur due to shading (Pook and Gill 1993). Foliage from the current year's growth was collected separately from foliage from previous years' growth because there are generally large differences between old and new foliar moisture content until the new foliage is fully matured (Chrosiewicz 1986; Keyes 2006). Old growth was sampled irrespective of needle age class but was generally less than 6 years old. All samples were collected in tin cans to avoid water loss and were kept cool after collection, and all laboratory measurements were made usually within 2 h on the day of collection.

Three 2-g 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 weight using a scale accurate to the nearest 10 mg. Samples were dried with lids off in a 95°C convection oven for 48 h. Cans were re-weighed after drying to determine dry weight. Can weights were also recorded and LFMC (percentage dry weight) was calculated using the following equation that removes the tare weight of the sample cans:

$$LFMC = ((FW - DW) \div (DW - TareW)) \times 100 \quad (2)$$

where *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 is mathematically equivalent to doing so (Zahn and Henson 2011). LFMC was converted from a dry weight basis to a wet weight basis using the following equation:

$$M_{wb} = (LFMC \times 100) \div (100 + LFMC) \quad (3)$$

where *M<sub>wb</sub>* is the equivalent percentage fresh weight moisture content. Conversion to fresh weight moisture content is convenient because it ensures that all the values used in the study are on the same 0 to 100 scale. *M<sub>wb</sub>* was used to calculate the water mass and dry mass on a fresh weight basis using the following equations:

$$WM = M_{wb} \div 100 \quad (4)$$

$$DM = 1 - WM \quad (5)$$

where *DM* is the dry mass for 1 kg of fresh needles and *WM* is the water mass contained in 1 kg of fresh needles.

### 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 1-g samples of needles and first measuring their fresh weight. Samples were then soaked for 24 h in distilled water, blotted dry using a paper towel and re-weighed for their turgid weight (TW). Samples were then dried for 48 h at 95°C in a convection oven. RWC (as a percentage of TW) was then calculated as follows:

$$RWC = ((FW - DW) \div (TW - DW)) \times 100 \quad (6)$$

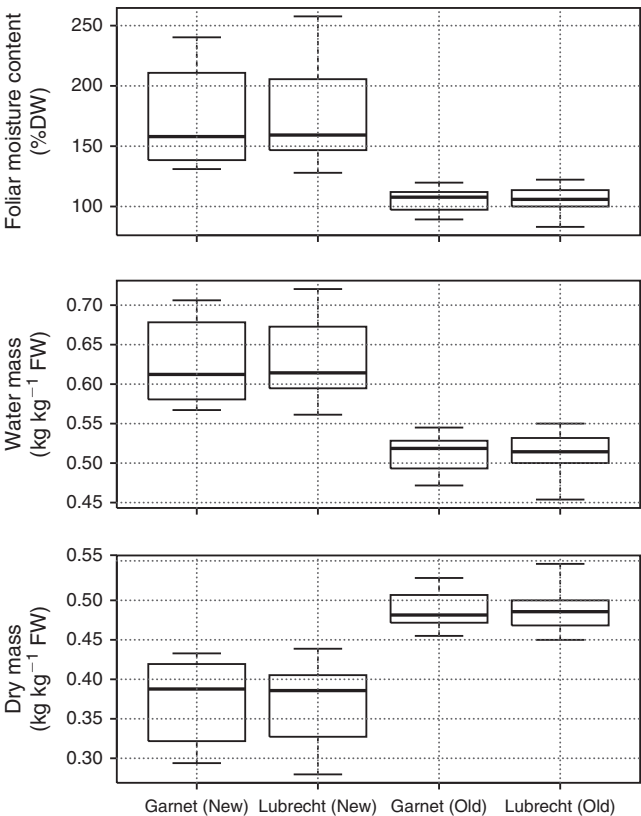
This value expresses the moisture content of the sample as a fraction of its saturated weight and is naturally bounded between 0 and 100.

### Foliar chemistry

Each week, a 20-g sub-sample was collected from the same foliar samples used to determine LFMC and RWC. New and old foliage was separated when both were present. Leaf chemical composition was determined using the wet reference method by an external foliage testing laboratory (AOAC 1984;

**Table 1.** Seasonal mean and standard deviations (in parentheses) of moisture content, relative water content and foliar chemistry for *P. contorta* foliage at both the Lubrecht and Garnet sampling sites for 2010 and 2011  
%DW, percentage dry weight; %TW, percentage turgid weight

|                               | New needles  |              |              |              | Old needles |              |              |             |
|-------------------------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|-------------|
|                               | Garnet       |              | Lubrecht     |              | Garnet      |              | Lubrecht     |             |
|                               | 2010         | 2011         | 2010         | 2011         | 2010        | 2011         | 2010         | 2011        |
| Foliar moisture content (%DW) | 169.5 (38.0) | 209.3 (11.6) | 172.8 (40.6) | 207.7 (10.1) | 105.5 (8.6) | 106.2 (13.7) | 104.0 (11.6) | 112.4 (7.4) |
| Relative water content (%TW)  | 84.5 (3.6)   | 83.4 (1.1)   | 85.1 (2.7)   | 83.8 (0.7)   | 77.0 (3.7)  | 77.5 (4.9)   | 75.2 (2.8)   | 72.6 (2.8)  |
| Fibre carbohydrates (%DW)     | 45.0 (2.4)   | 52.3 (10.4)  | 43.9 (2.7)   | 48.4 (9.0)   | 40.6 (2.0)  | 43.7 (5.6)   | 39.4 (2.1)   | 42.8 (6.6)  |
| Non-fibre carbohydrates (%DW) | 40.7 (2.3)   | 34.3 (9.8)   | 42.6 (2.3)   | 38.7 (9.4)   | 41.9 (2.4)  | 37.8 (6.5)   | 42.4 (2.2)   | 39.2 (6.9)  |
| Starch and sugar (%DW)        | 8.5 (2.8)    | 6.9 (1.4)    | 9.7 (2.7)    | 7.5 (1.7)    | 15.9 (2.1)  | 17.8 (2.1)   | 18.1 (2.3)   | 16.0 (1.7)  |
| Crude fat (%DW)               | 4.0 (1.2)    | 2.9 (0.3)    | 3.6 (1.0)    | 2.8 (0.5)    | 7.5 (0.7)   | 8.2 (0.9)    | 8.6 (0.5)    | 8.3 (1.1)   |
| Protein (%DW)                 | 8.4 (2.0)    | 8.2 (2.3)    | 8.0 (1.9)    | 8.2 (1.8)    | 7.8 (2.2)   | 7.1 (3.2)    | 7.2 (2.4)    | 7.3 (2.4)   |
| Ash (%DW)                     | 2.0 (0.29)   | 2.3 (0.14)   | 1.9 (0.20)   | 1.8 (0.15)   | 2.2 (0.35)  | 3.2 (0.36)   | 2.4 (0.30)   | 2.4 (0.32)  |



**Fig. 1.** Measured live foliar moisture content, calculated water mass and calculated dry mass for the Lubrecht and Garnet sample sites for both new and old foliage. %DW, percentage dry weight; FW, fresh weight.

Horwitz and Latimer 2000; <http://www.agrianalysis.com/>, accessed 10 March 2014). The analysis provided measurements of neutral detergent fibre (fibre carbohydrates) (NDF), non-fibre carbohydrates (NFC), crude fat (CF), crude protein (CP) and ash content (AC). Additional measurements of total non-structural

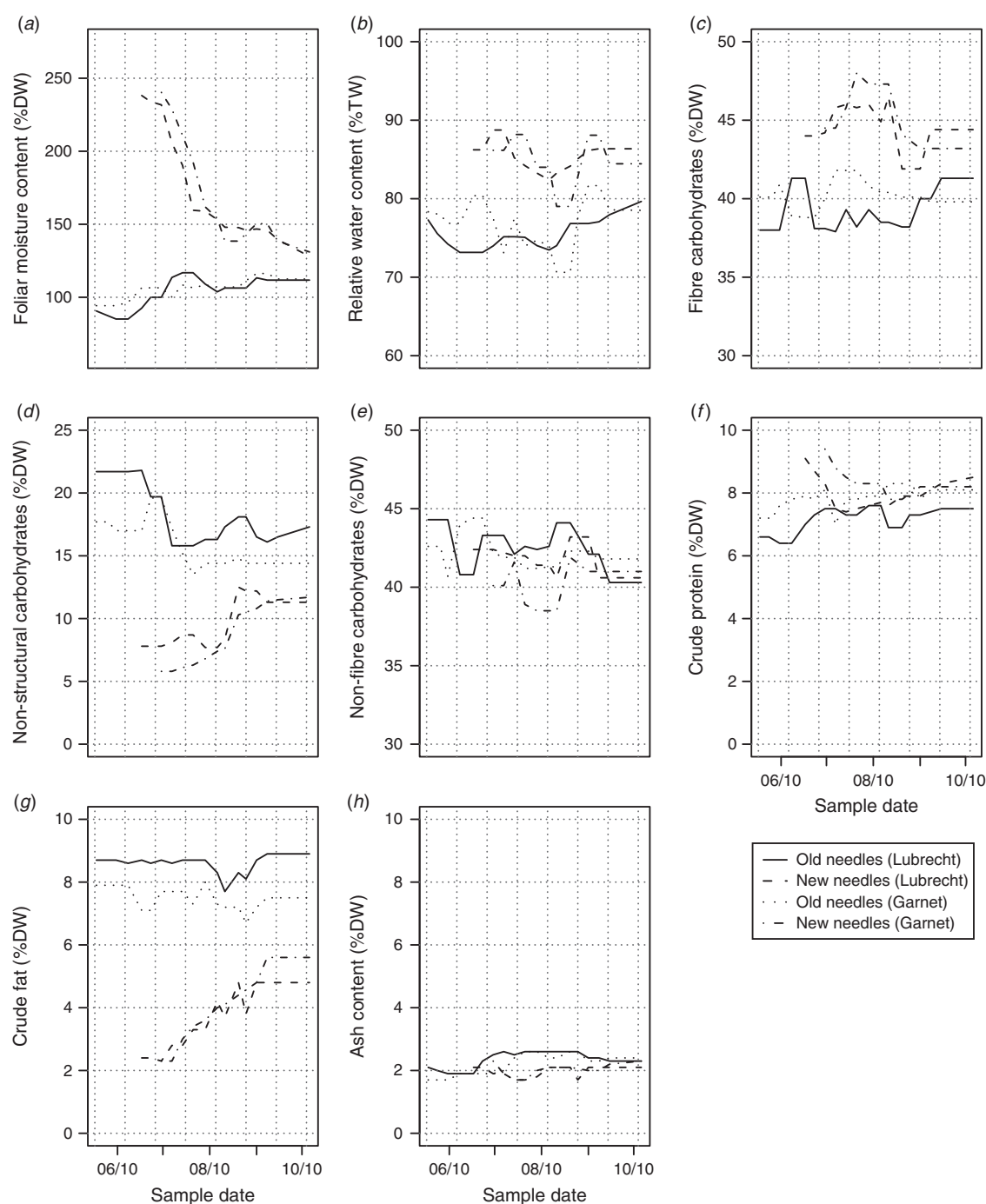
carbohydrates (NSC) were also made using standard wet chemistry methods (AOAC 1984). CP was determined using a TruSpec combustion analyser (ANKOM Technologies, Macedon, NY, USA). CF was determined using an ANKOM fat analyser (ANKOM Technologies) with petroleum ether. NDF was determined using an ANKOM 200 fibre analyser (ANKOM Technologies). NFC were calculated by the difference method using the following equation:

$$NFC = 100 - NDF + CF + CP + AC \tag{7}$$

The NDF analysis quantifies structural carbohydrates such as cellulose, hemicellulose and lignin, whereas NFC are generally water soluble and represent primarily sugars, starches, and other non-structural carbon compounds in the leaves. NSC are a component of NFC and are composed of starch and simple sugars. CP is generally proportional to the amount of nitrogen in each sample. CF expresses the quantity of isoprenoids, waxes and oils present in the foliage and AC quantifies the mineral content of the needle (Kozłowski and Pallardy 1979).

Data analysis

All data analysis was performed using the R statistical software package, version 2.15.5 (R Foundation for Statistical Computing, Vienna, Austria, see <http://www.R-project.org/>). Analysis of variance was used to assess differences in predictive variables across sites, needle age categories and sample years. Pearson’s correlations were used to explore the relationships between foliar chemistry, RWC and LFMC. The best-fit model for predicting water mass as a function of RWC was determined using ordinary least-squares (OLS) regression. The best-fit model for predicting dry mass changes as a function of foliar chemistry was determined using a stepwise, OLS regression. These two combined models were then used to predict water mass and dry mass separately and these predictions were used to calculate LFMC based on Eqn 1. Final predictions of LFMC were correlated with field-measured LFMC using a standard Pearson’s correlation.



**Fig. 2.** An example of the seasonal variations in foliar moisture content, relative water content and six chemical component of *Pinus contorta* foliage from May to October 2010 for the Lubrecht and Garnet sample sites for both new and old foliage. Strong declines in the foliar moisture content (a) of new needles at both sites correspond to increases in non-structural carbohydrates (starch and sugar content) (d) and crude fat of the foliage (g). Relative water content was stable throughout the season but varied between needle ages (b). New needles were composed of a higher percentage of fibre carbohydrates (c) but had approximately the same non-fibre carbohydrate percentage as old needles (e). Crude protein declined slightly in new needles during the early part of the growing season but eventually matched that of old needles by August (f). Ash content (h) showed little variation between old and new needles for either site. %DW, percentage dry weight; %TW, percentage turgid weight.

## Results

Foliar moisture and chemistry was significantly different between needle age categories for all but NFC (Table 1). LFMC,

fibre and NFC and AC were significantly different between sample years. Only CP was significantly different between sampling sites.



**Table 2.** Results of the ordinary least-squares regression model fit predicting foliar water mass (kg water kg<sup>-1</sup> fresh mass) as a function of relative water content  
\*\*, *P* < 0.01; \*\*\*, *P* < 0.001

|                        | Coefficient | Intercept  | <i>F</i> -statistic | <i>R</i> <sup>2</sup> |
|------------------------|-------------|------------|---------------------|-----------------------|
| Relative water content | 0.99499***  | −0.22950** | 106.3***            | 0.59                  |

**Table 3.** Results of ordinary least-squares regression model fit predicting foliar dry mass (kg dry mass kg<sup>-1</sup> fresh mass) as a function of foliar chemistry  
Non-structural carbohydrates and crude fat were the best predictors of foliar dry mass: \*\*\*, *P* < 0.001

|                              | Coefficient | Intercept   | <i>F</i> -statistic | <i>R</i> <sup>2</sup> |
|------------------------------|-------------|-------------|---------------------|-----------------------|
| Non-structural carbohydrates | 0.007320*** | 0.252990*** | 253.8***            | 0.87                  |
| Crude fat                    | 0.013706*** |             |                     |                       |

Boxplots of measured LFMC, calculated water mass and calculated dry mass for the Lubrecht and Garnet sample sites for both new and old foliage are shown in Fig. 1. LFMC and water mass were highest for new foliage at both sites and lowest in old foliage. Conversely, dry mass was highest in old foliage and lowest in new foliage at both sites. Old needles have approximately equal amounts of water and dry matter and exhibit less variability than do new needles.

Seasonal mean and standard deviations for LFMC, RWC and six foliage chemistry groups for all sites, needle age classes and sample years are shown in Table 1. Average LFMC, RWC, NDF and protein were higher in new foliage than in old foliage. In contrast, old foliage had higher percentages of NFC, including starch and sugar, and CF. Strong seasonal declines in LFMC content were noted for new needles at both sites (Fig. 2). These changes were concurrent with a slight increase in LFMC of old needles at both sites. In contrast, RWC showed no strong seasonal decline, but did show seasonal minimums during late summer when water stress would likely have been highest (Fig. 2b). New needles were composed of proportionally more NDF than were old needles but had relatively consistent percentages of NFC across both new and old needles for both sites. Sugar and starch content of new needles doubled over the growing season and CF content of new needles tripled. Protein and AC was little changed throughout the season.

Variations in water mass were strongly related to variations in RWC ( $\rho = 0.77$ ) (Fig. 3a). Dry mass variations were positively correlated with seasonal changes in NSC ( $\rho = 0.91$ ) (Fig. 3b), CF ( $\rho = 0.91$ ) (Fig. 3c), and AC ( $\rho = 0.31$ ) and negatively correlated with neutral detergent fibre (cellulose and lignin) ( $\rho = -0.56$ ) and CP ( $\rho = -0.63$ ). Correlations between NFC and LFMC were not significant.

RWC explained 59% of the variation in foliar water mass (OLS,  $P < 0.001$ ,  $F = 106.3$ ,  $R^2 = 0.59$ ,  $n = 77$ ) (Table 2). NSC (total of starches and sugars), CF and CP were selected as the best predictors of seasonal dry weight changes in the backward, stepwise OLS regression. However, when the stepwise model was examined, CP was not significant so it was excluded as a

predictor. The final model was fit with only NSC and CF (Table 3). These two variables explained 87% of the variations in dry mass (OLS,  $P < 0.001$ ,  $F = 253.8$ ,  $R^2 = 0.87$ ,  $n = 77$ ).

These two fitted models were then used to predict water mass and dry mass and these predictions were used to calculate LFMC based on Eqn 1. The results of the predictions of water mass, dry mass and subsequent foliar moisture content are show in Fig. 4. LFMC (%DW) was then predicted as the ratio of the two linear models presented in Tables 2 and 3:

LFMC

$$= \frac{0.99499 \times RWC - 0.22950}{0.007320 \times NSC + 0.013706 \times CF + 0.252990} \times 100 \tag{8}$$

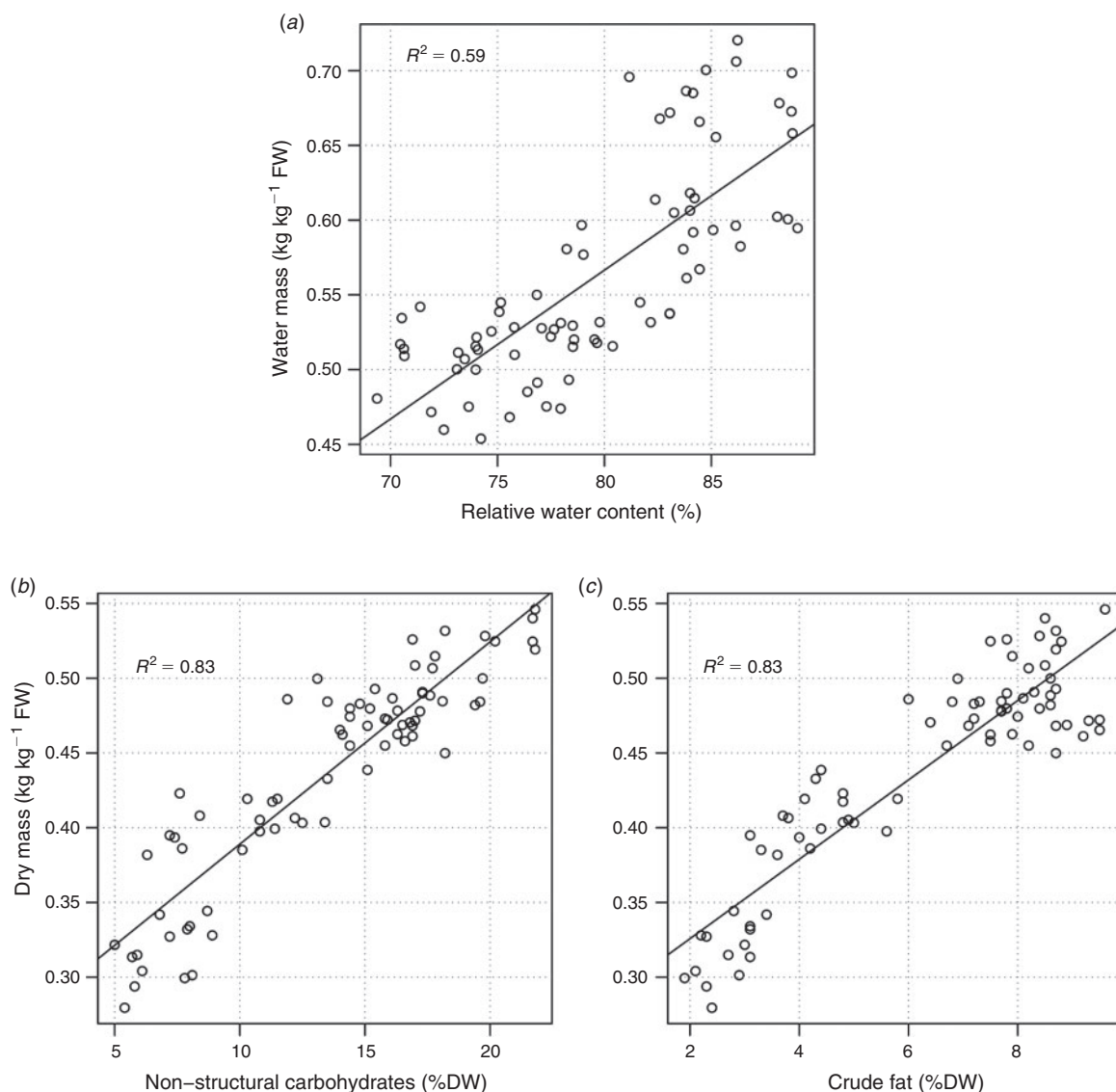
where RWC is a percentage and NSC and CF are percentage dry weights. This decoupled model explained 85% of the variation in LFMC.

Discussion

LFMC has long been recognised 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 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 changes both in the actual water content of the foliage and in the dry weight of the foliage. Additionally, they emphasise 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 LFMC 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. 2007b). However, these studies have had limited or mixed success. For example, Pellizzaro et al. (2007b) found strong correlations between LFMC and five drought indices for some Mediterranean shrub species during periods of water stress, but poor correlations as drought stress was relieved. Also, Dimitrakopoulos and Bemmerzouk (2003) found that although drought indices closely match the moisture content of herbaceous plants, they were poorly correlated with the foliar moisture content of deep-rooted *P. brutia* trees. De-coupling the effects of water stress from seasonal dry matter changes would have likely strengthened these studies.

LFMC can be divided into two separate, yet complimentary components as expressed in Eqn 1. The changes in the absolute mass of the water (numerator of Eqn 1) should be most related to the water cycle of the trees and can be directly linked to the soil–vegetation–atmosphere continuum (Nelson 2001) (Fig. 3). It is regulated by all the factors that dictate the rate of water uptake from the soil, transport to the leaves and loss through the foliar stomata. There is a close relationship between leaf water potential and RWC in *P. contorta* (Running 1980). Ecosystem process models, such as Biome-BGC (Running and Hunt 1993),



**Fig. 3.** Best-fit relationships between foliar water mass and relative water content (a) and between dry mass and non-structural carbohydrates (b) and crude fat (c) across all sample sites, years and needle ages. Relative water content explains 59% of the variation in water mass, whereas non-structural carbohydrates and crude fat each explain 83% of the variation in dry mass. Plots are shown with ordinary least-squares regression lines for reference. %DW, percentage dry weight; FW, fresh weight.

predict leaf water potential as a function of variations in weather and consequently may be useful in predicting seasonal changes in live fuel moisture. The second component of LFMCI is the dry matter change (denominator of Eqn 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 NSC and foliar dry mass. Ultimately, attempts to better understand the dynamics of LFMCI must consider both water mass and dry mass changes and their driving factors to adequately describe these seasonal changes. Existing physiologically based process models may be able to explore and model many of these relationships.

Our results show that the moisture contents of new and old needles are significantly different throughout most of the growing season. However, these two foliar components are often not separated at sampling and they may be combined into a single sample during collection (e.g. Castro *et al.* 2003; Pellizzaro *et al.* 2007b). This sampling strategy would explain why reported seasonal LFMCI 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 high moisture contents, and old foliage with lower moisture contents. Others have demonstrated the large discrepancies in moisture content between new and old foliage (Agee *et al.* 2002; Chrosciewicz 1986) and have suggested the need to separate the two categories when sampling. Our results extend these studies

**Table 4.** Summary *F*-statistics and *P*-values for analysis of variance between foliar moisture content, relative water content, foliar chemistry, sample site, needle age and sample year\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; NS, not significant. %DW, percentage dry weight; %TW, percentage turgid weight

| Variable                      | Sampling site (Garnet or Lubrecht) | Needle category (new or old) | Year (2010 or 2011) |
|-------------------------------|------------------------------------|------------------------------|---------------------|
| Foliar moisture content (%DW) | 0.907 (NS)                         | 146.932***                   | 5.318*              |
| Relative water content (%TW)  | 0.552 (NS)                         | 135.876***                   | 1.144 (NS)          |
| Fibre carbohydrates (%DW)     | 1.58 (NS)                          | 38.95***                     | 15.66***            |
| Non-fibre carbohydrates (%DW) | 0.116865 (NS)                      | 0.855 (NS)                   | 14.925***           |
| Starch and sugar (%DW)        | 0.106 (NS)                         | 208.222***                   | 1.375 (NS)          |
| Crude fat (%DW)               | 0.728 (NS)                         | 439.904***                   | 1.077 (NS)          |
| Protein (%DW)                 | 8.522**                            | 29.654***                    | 0.545 (NS)          |
| Ash (%DW)                     | 0.605 (NS)                         | 22.334***                    | 7.939**             |

by showing the large differences in dry matter composition between old and new needles, and reinforce the need to separate new and old foliage when examining their seasonal dynamics (Table 4).

Fire behaviour models are often used to assess the likelihood that a fire will carry from the surface into the tree crowns and these models require conifer LFMC direct input (Van Wagner 1977). These models only allow a single foliar moisture content input, yet our study and several others have shown that new and old foliage have significantly different moisture contents. To illustrate the importance of this difference, we applied the Van Wagner transition to crown fire model, as implemented in the BehavePlus fire modelling system (Andrews 2013), to our mean foliar moisture contents for both new and old needles (177 and 105%) assuming a canopy base height of 3 m and a surface fire flame length of 2 m. The model indicates that surface fires could transition to crown fires in old foliage but not in new foliage. This makes the application of such a model to trees with a combination of new and old foliage problematic. Future measurements of foliar moisture content for use in fire behaviour models must either separate the contributions of new and old foliage to crown fire potential or they must develop canopy-scale metrics of foliar moisture content that are weighted based on the biomass proportions of new and old needles within the trees. This has also been suggested by Agee and others (Agee *et al.* 2002). Understanding the timing of needle flushing, rate of needle elongation, rate of needle hardening and the total tree foliar biomass proportions of new and old needles would allow us to better assess canopy-scale foliar moisture content and would provide more meaningful inputs to fire behaviour models.

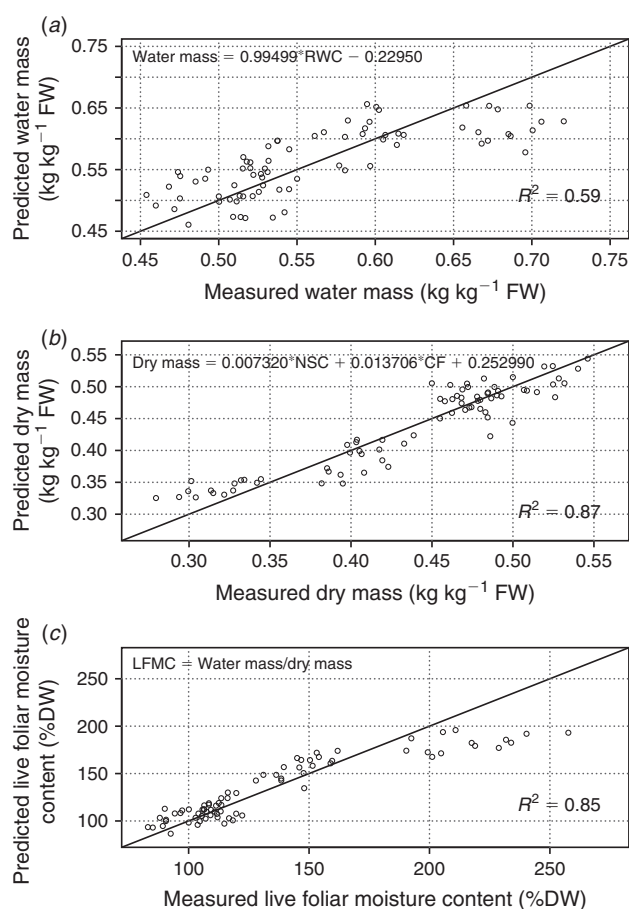
Changes in dry matter are likely a dynamic combination of foliar development, photosynthesis, respiration and carbon allocation. During the early period of development, we saw large declines in new needle foliar moisture content and slight increases in the moisture content of old needles. These changes were observed concurrent with continuous increases in the NSC and CF of new needles and slight declines of those chemical components in old 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 to increase (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 the plant several weeks after they are fully developed (Ericsson 1978). Thus, greater understanding of physiological drivers that control the dry matter changes in live fuels could allow us to better seasonally predict dry matter content.

Considerable interest has been paid to the remote estimation of LFMC 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 LFMC 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 water content and plant dry matter differences (Bowyer and Danson 2004). Thus, a better understanding of the individual dynamics of plant water content and foliar dry matter content may help improve our ability to more adequately assess LFMC by remote sensing.

All the relationships between foliar chemistry, water mass and dry mass were modelled as linear but some non-linear relationships were noted, which biased the model to under-predict LFMC above ~190% (Fig. 4). Much of this bias was driven by a non-linear relationship between RWC and water mass at high RWC (>80%). The highest RWC was measured in new needles that had not yet fully matured. New needle structure was changing over time, evidenced by the increases observed in CF and NSC of new needles during the development period (Fig. 2d, g). In contrast, needle contents of old needles were changing, whereas their structure remained static. This suggests that a more complete model of the relationship between RWC and water mass may include some proxy for needle development. This may eliminate some of the non-linearity that we observed and it would improve the prediction of LFMCs across the full range of observed values.

There has been considerable interest over recent decades to assess the differences in flammability across various plant species, but studies have not considered the differences in overall plant chemistry between species (Dimitrakopoulos and Papaioannou 2001; Pellizzaro *et al.* 2007a). This may be important because both water content and dry matter composition are important factors in fuel flammability (Finney *et al.* 2013). While water limits the rate of fuel preheating, dry matter



**Fig. 4.** Scatterplot of calculated and predicted water mass (a), dry mass (b) and final live foliar moisture content (c) for *P. contorta* foliage across all sample sites, years and needle ages. Relative water content explained 59% of the variation in foliar water mass, whereas non-structural carbohydrates and crude fat explain 87% of the variation in foliar dry mass. The combined predictions of water mass and dry mass explained 85% of the variation in live foliar moisture content (c). site. %DW, percentage dry weight; FW, fresh weight.

provides the source of gases that supports flames. Inter- and intra-species differences in plant chemistry that manifest themselves as differences in the apparent moisture content of the fuels may have a direct effect on the flammability of vegetation beyond the simple moisture and preheating relationships. For example, we noted large differences between the CF content of new and old *P. contorta* needles and CF can significantly influence the heat content of the fuel (Philpot 1969). Ultimately, describing the variations in water mass, dry mass and subsequent LFMC both within and between species may improve our ability to assess how living plants influence wildland fire behaviour.

In this paper, we have presented the model results from a common Intermountain conifer species and we have shown that this method adequately describes the observed seasonal variations in *P. contorta* LFMC. However, this method is sufficiently general and should allow the examination of the seasonal dynamics of other species. More work should be done to better understand how this study could be applied to other species and

to assess whether these relationships are consistent across a broad range of plant functional types.

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

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