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Keywords

Aboveground biomass production, grassland species composition, hyperspectral remote sensing, leaf traits, NDVI, plant functional groups

Disciplines

Ecology and Evolutionary Biology | Plant Sciences | Remote Sensing

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ORIGINAL RESEARCH

Spectrally derived values of community leaf dry matter content link shifts in grassland composition with change in biomass production

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Abstract

Leaf traits link environmental effects on plant species abundances to changes in ecosystem processes but are a challenge to measure regularly and over large areas. We used measurements of canopy reflectance from grassland communities to derive a regression model for one leaf trait, leaf dry matter content (LDMC). Partial least squares regression (PLSR) analysis was used to model community-weighted (species abundance-weighted) values of LDMC as a function of canopy reflectance in visible and near-infrared (NIR) wavebands. The PLSR model then was applied to airborne measurements of canopy reflectance to determine how community LDMC interacts with inter-annual variation in precipitation to influence the normalized difference vegetation index (NDVI), a surrogate of aboveground biomass production, of restored grassland during spring over 4 years. LDMC was well-described by a PLSR model that included reflectance measurements located primarily in red edge and NIR portions of the spectrum. Community LDMC decreased as annual forb species became more abundant and was negatively correlated with maximum values of NDVI. Decreased precipitation reduced NDVI (biomass production) both by increasing community LDMC (LDMC response) and reducing the slope of the NDVI-LDMC relationship (LDMC effect on NDVI). We find that grassland LDMC is well-described by a regression model using canopy reflectance in red edge and NIR wavebands. Our results demonstrate the utility of spectral estimates of LDMC for discerning shifts in grassland composition and predicting consequences for production-related ecosystem functions.

Introduction

Plant science was advanced substantially by the demonstration of a tradeoff between leaf life span and rates of resource acquisition and use (leaf economics spectrum; Wright et al. 2004; Reich 2014; Díaz et al. 2016). Exploitative species exhibit rapid rates of growth, resource acquisition and leaf turnover. Conservative species are characterized by slower rates of growth and turnover. This tradeoff in growth strategies among species is linked to differences in leaf structural and chemical traits. Exploitative species are characterized by thin leaves with low values of leaf dry matter content (LDMC; ratio of leaf dry mass to leaf saturated mass) and high element

concentrations (Reich 2014; Díaz et al. 2016). Conservative species, by contrast, typically have thicker leaves with high values of LDMC. Growth rate and LDMC, therefore, frequently are negatively correlated. One implication is that LDMC may prove a reliable predictor of plant production or other ecosystem processes when scaled to the plant community level by weighting species values of LDMC by their abundances. Garnier et al. (2004), for example, demonstrated that grassland production per unit of green biomass declined as community LDMC increased. Community LDMC thus provides a mechanistic link between variation in plant species abundances and aspects of ecosystem functioning (Lavorel and Garnier 2002; Lavorel et al. 2013).

Community LDMC operates both as an ‘effect’ and ‘response’ trait (Lavorel and Garnier 2002; Suding et al. 2008). Community LDMC operates as a response trait when environmental or management changes drive phenotypic variation in species trait values or in the composition or abundances of species that differ in LDMC (Jung et al. 2010). For example, disturbances such as heavy grazing favor grassland plants with low LDMC that grow earlier and reach peak biomass sooner than species with higher LDMC (Duru et al. 2009; Moretti et al. 2013). Community LDMC operates as an effect trait when it influences consequences of environmental variation for plant production or other ecosystem processes (Garnier et al. 2004). For example, plant production typically is greater in low- than high-LDMC communities (e.g. Garnier et al. 2004; Moretti et al. 2013), although the opposite may be true when physical conditions are severe (Zhu et al. 2016). Conversely, variability in production is less sensitive to inter-annual variation in precipitation in high- than low-LDMC communities (Polley et al. 2013).

Community LDMC can provide insight into the contributions of differences or change in plant communities to ecosystem processes. However, LDMC is a challenge to measure frequently and over large areas. Traditional field-based measurements of community LDMC are expensive and labor-intensive. Airborne remote sensing demonstrates promise as a cost-efficient option to assess community biochemical traits at temporal and spatial scales at which environmental and management drivers operate, but has proven less effective in discerning biophysical traits, such as LDMC (Homolová et al. 2013; Van Cleemput et al. 2018). This gap is particularly evident for grasslands.

Remotely sensed estimates of LDMC and related mass-based traits (e.g. leaf mass per unit of leaf area; LMA) usually are derived using those portions of the spectrum in which leaf dry matter most strongly influences reflectance. Wavebands in the short-wave infrared (SWIR) spectrum (1200–2500 nm) have been shown to be diagnostic of variation in LDMC and LMA (Casas et al. 2014; Chadwick and Asner 2016; Ali et al. 2017). LDMC of forest species correlated most strongly with reflectance at 2300 nm, for example (Ali et al. 2016). However, there is evidence that dry matter content also covaries with reflectance in the visible and near-infrared (NIR) regions of the spectrum. Wang et al. (2011), for example, found that increasing LMA reduced leaf reflectance in the red-edge region of the spectrum, beginning at 700 nm. Others have detected strong signals in the red and red-edge regions of the spectrum for LMA variation among leaves of forest (Chadwick and Asner 2016) and agronomic species (Ely et al. 2019). Leaf mass is a component of both LMA and LDMC. Consequently, LMA and LDMC usually are positively correlated within species (Puglielli et al. 2019) and

when assessed across large spatial scales (Messier et al. 2017). This correlation between the two traits implies that variation in LDMC, as in LMA, may be linked to reflectance differences in visible and NIR wavebands. Spectroradiometers capable of measuring reflectance in this spectral range currently are less expensive and more readily deployed using an unmanned aerial vehicle (UAV) than are sensors that cover the full visible through SWIR spectral range. There are, therefore, economic as well as practical incentives to model community LDMC using the visible to NIR reflectance spectrum. Yet, we know no published documentation of such a model.

Our primary objectives were to develop a statistical model for community LDMC applicable at the field scale and determine how community LDMC interacts with inter-annual change in precipitation to influence plant biomass production, as indicated by the normalized difference vegetation index (NDVI), in restored perennial grassland. We used hyperspectral measurements of leaf and canopy reflectance in visible and NIR bands to model grassland LDMC. Models were developed using partial least squares regression analysis (PLSR). The resulting canopy model was applied to 4 years of reflectance measurements collected during spring to predict the community LDMC. We further evaluated the response of community LDMC to inter-annual variation in precipitation and effect of community LDMC on NDVI. Consistent with previous findings (e.g. Garnier et al. 2004; Moretti et al. 2013; Polley and Wilsey 2018), we predicted that inter-annual variation in precipitation would change both community LDMC (LDMC response) and the relationship between NDVI and LDMC (LDMC effect on NDVI).

Materials and Methods

Site and vegetation

We used measurements of spectral reflectance to calculate species abundance-weighted values of community LDMC in restored grassland located in Temple, Texas, USA (31° 10' N, 97° 34' W). Eight randomly selected stands, each 17 m wide and 137–218 m long (0.26–0.37 ha), were restored to grassland in 2010 by planting a mixture of native perennial forb and grass species in a former agricultural field (Long-term Biomass Experiment; LTBE). Stands traverse a catena from a silty clay soil on the upland (Austin series; 43% clay) to a clay soil on the lowland (Houston Black series; 52% clay). Remaining stands (16) in LTBE were planted to a monoculture of the C₄ grass *Panicum virgatum* L. (switchgrass; cultivar ‘Alamo’). Thirteen 7-m diameter patches were permanently located along the upland to lowland catena in each stand of restored grassland (52 patches per soil type). Restored

grassland was not grazed or fertilized but is hayed annually following the growing season.

The realized vegetation in restored grassland is strongly influenced by a group of approximately 25 annual grass and forb species that invaded following restoration. Most annual species are small-statured, cool season (C_3) plants that establish following rainfall in autumn and complete growth during spring. Dominant species of annuals include the forbs *Gaillardia pulchella* Foug and *Monarda citriodora* Cerv. ex Lag and grass *Bromus japonicus* Thunb. ex Murray.

Field measurements

Biomass per unit of surface area was estimated for each of 32 randomly selected patches in spring 2016 by averaging aboveground harvests from two 1×1 m plots per patch. Species composition of restored grassland was measured in randomly chosen 7-m diameter patches during April–May 2017. Cover per species and of bare soil was estimated visually in each of eight, 76-cm diameter plots that were randomly located in each of 8 patches on each soil type.

LDMC (%) was measured on 52 single-species stands (canopies) centered in 30-cm diameter rings during March–May 2016 and 2017 (Table 1) and on 41 samples of individual leaves during March–May 2016 (Table S1). Canopy samples included stands of 40 unique species and 2 replicate stands for each of 12 of the 40 species. Canopy traits in addition to LDMC vary among species. Replicate measurements of 12 species were included in order to incorporate variation in LDMC (ecotypic or phenotypic variation within species) that was independent of differences in canopy structure among species. Leaf samples included 37 unique species and 2 replicate leaves for each of 4 species. LDMC was measured on fully expanded single leaves (leaf samples) or groups of leaves (3–7 leaves; canopy samples) in the upper canopy of each species using methods outlined by Cornelissen et al. (2003). Leaves were collected from species within LTBE stands and from adjacent woodlands and experimental grassland plots (Wilsey et al. 2011; Polley et al. 2019) to capture the range of LDMC values represented in the local area. We collected canopy samples from five functional groups of species, including C_4 perennial grasses, C_3 perennial grasses, C_3 annual grasses, C_3 annual forbs and C_3 perennial forbs. Samples of individual leaves included woody species.

Reflectance was measured at several spatial scales. We measured reflectance from 7-m diameter patches in restored grassland, grassland plots on which species cover was estimated, single-species stands and individual leaves of different species. Reflectance was measured immediately prior to quantifying species cover or collecting leaves to determine LDMC. Each reflectance measurement

Table 1. Leaf dry matter content (LDMC) of upper leaves from single-species stands (canopies) for which spectral reflectance was measured ($n = 52$ samples). Measurements were used to develop a partial least squares regression model relating LDMC to canopy reflectance. Replicate stands for a given species are distinguished by the number in parentheses following the species name. Sampled species segregate into five functional groups

Group/species	LDMC (%)
Annual forbs	
<i>Gaillardia pulchella</i>	11.9
<i>Chichorium intybus</i>	13.4
<i>Lindheimera texana</i>	14.1
<i>Rapistrum rugosum</i>	15.3
<i>Lactucea serriola</i>	15.9
<i>Monarda citriodora</i>	17.7
<i>Ambrosia trifida</i>	17.8
<i>Oenothera speciosa</i>	20.3
<i>Helianthus annuus</i>	21.5
<i>Daucus pusillus</i>	22.6
Perennial forbs	
<i>Ratibida columnifera</i>	15.3
<i>Vernonia baldwinii</i>	17.4
<i>Medicago lupulina</i>	20.0
<i>Solidago canadensis</i>	20.4
<i>Helianthus maximiliani</i>	22.7
<i>Medicago sativa</i>	22.9
<i>Solanum dimidiatum</i>	23.3
Annual grasses	
<i>Lolium perenne</i>	19.2
<i>Bromus japonicus</i>	23.2
<i>Triticum aestivum</i>	27.4
C_3 perennial grasses	
<i>Festuca arundinacea</i>	27.7
<i>Nassella luecotricha</i> (1)	39.1
<i>Nassella luecotricha</i> (2)	46.3
C_4 perennial grasses	
<i>Paspalum dilatatum</i>	24.1
<i>Tripsacum dactyloides</i> (1)	24.5
<i>Tripsacum dactyloides</i> (2)	25.7
<i>Panicum virgatum</i> (cultivar 'Alamo')	26.5
<i>Panicum coloratum</i> (1)	28.1
<i>Eriochloa sericea</i>	28.5
<i>Bothriochloa ischaemum</i> (1)	30.5
<i>Sorghum halepense</i> (1)	30.6
<i>Bothriochloa ischaemum</i> (2)	30.6
<i>Sorghastrum nutans</i> (1)	31.8
<i>Cynodon dactylon</i> (1)	32.6
<i>Sorghum halepense</i> (2)	32.6
<i>Bothriochloa laguroides</i> (1)	33.4
<i>Andropogon gerardii</i>	33.7
<i>Sorghastrum nutans</i> (2)	35.1
<i>Panicum coloratum</i> (2)	36.2
<i>Bothriochloa laguroides</i> (2)	37.3
<i>Sporobolus compositus</i> (1)	38.8
<i>Panicum virgatum</i> (upland cultivar)	38.9
<i>Schizachyrium scoparium</i>	38.9
<i>Cynodon dactylon</i> (2)	41.9

(Continued)

Table 1. Continued.

Group/species	LDMC (%)
<i>Eragrostis curvula</i> (1)	42.5
<i>Sporobolus compositus</i> (2)	42.9
<i>Bouteloua curtipendula</i> (1)	44.0
<i>Buchloe dactyloides</i> (1)	44.2
<i>Eragrostis curvula</i> (2)	46.4
<i>Buchloe dactyloides</i> (2)	49.5
<i>Bouteloua hirsuta</i>	50.7
<i>Bouteloua curtipendula</i> (2)	56.4

represents the mean of three consecutive samplings of reflectance. Reflectance from intact leaves was measured with the ASD Fieldspec 3 (ASD Inc., Boulder, CO, USA) using the light source associated with the ASD Inc. 'leaf clip'. Reflectance was measured on leaves that were large enough to fill the 'leaf clip'. Leaves of several species for which canopy reflectance was measured were too small. We augmented the number of leaf-level readings by measuring LDMC and reflectance on the 'larger' leaves of several woody species (Table S1). Reflectance from grassland patches, plots on which species composition was determined, and single-species canopies was measured using an ASD HandHeld2 Pro spectroradiometer (spectral range of 350–1070 nm). Our goal in measuring both individual leaves and single-species canopies was to determine whether LDMC could be modeled at the two scales using similar wavebands.

Reflectance from leaves, plots and single-species stands was measured from ground level. Reflectance per patch was measured from an aerial platform [UAV, S1000; DJI; Shenzhen, China]. Patch reflectance was measured by flying the GPS-guided, rotary-wing UAV with the ASD HandHeld2 Pro spectroradiometer mounted beneath to a stationary position at 15.8 m height (25° field of view) above each patch. All measurements of reflectance were collected on cloudless days within 2 h of solar noon and referenced to a Spectralon® white reference panel. Reflectance was calculated by dividing radiance reflected from the plant canopy by radiance incident on the canopy. Incident radiation was considered the radiant flux reflected from a Spectralon® white reference panel exposed to full sunlight.

Data from the 350–1050 nm spectral range were used in all analyses. We used reflectance values from 5-nm intervals, beginning at 660 nm and ending at 760 nm, and 10-nm intervals over the remainder of the 350–1050 nm spectrum, resulting in a total of 80 wavebands. Reflectance data for the 80 wavebands per patch were normalized to a uniform brightness of 1 (Brightness normalization; Feilhauer et al. 2010) to dampen the influence of canopy shading on model fits.

PLSR models

PLSR was used to model LDMC as a function of spectral reflectance from single leaves and canopies of single-species stands on which LDMC was measured. Leaf and canopy LDMC were modeled separately using SAS 9.4 (Cary, NC, USA). PLSR represents reflectance from all wavebands using a reduced set of uncorrelated latent variables (Wold et al. 2001). This technique has proven valuable in linking the reflectance spectrum to leaf chemical and physical properties (e.g. Chadwick and Asner 2016; Martin et al. 2018). We used a 'cross validation' procedure to determine the number of latent variables required to predict LDMC (Shao 1993). Models were developed using data from the 52 single-species canopies or 41 individual leaves. A PLSR model was fit to a data set composed of every seventh entry in each data set (52 canopies; 41 leaves), beginning with the first data entry, while minimizing the prediction error for unfitted data. The process was repeated iteratively by beginning the procedure with the second data entry, then third entry, etc. through each successive entry in each data set. We chose the PLSR model with the least number of latent variables for which the residuals from predictions of unfitted data (root mean predicted residual sum of squares; PRESS) did not differ significantly from the model with minimum PRESS. We then tested the utility of PLSR models for LDMC that used fewer than the complete data set of 80 wavebands to determine latent variables. Wavebands for which values of the Variable Influence on Projection (VIP; Wold et al. 2001) were < 0.8 were deleted iteratively to identify statistically significant PLSR models that employed the fewest wavebands to develop latent variables.

Model evaluation and application

The PLSR model that was developed with data from single-species stands (canopies) was used to estimate community LDMC at the patch scale (7-m diameter). Consistency in LDMC prediction on scaling in space from smaller scales to the patch scale was tested by comparing community LDMC modeled from patch-scale reflectance to the average value of LDMC modeled using reflectance measurements from the eight plots sampled for species composition per patch. Model utility in estimating community LDMC was tested by comparing predicted LDMC to the functional group composition of communities sampled in 76-cm diameter plots. Differences in LDMC among plots should reflect differences in the contributions of groups of species for which LDMC is largely confined to extremes of the range measured (e.g. annual forbs).

Community LDMC-NDVI relationships were assessed using NDVI calculated for each plot and patch for which reflectance was measured. NDVI was calculated by

dividing the difference in reflectance between NIR and red wavebands by the sum of reflectance in NIR and red bands. Aboveground biomass was assumed to be a positive function of community NDVI at the patch scale. To test this assumption, we evaluated the relationship between biomass harvested from each of 32 patches in spring 2016 and patch NDVI.

Statistics

Linear regression analysis was used to describe relationships between community LDMC and both abundances of functional groups of species and NDVI. Year and soil effects on the slopes of linear regression relationships between NDVI and LDMC were compared with the F statistic (Weisberg 1980). Regressions were fit using SAS 9.4.

Results

LDMC measurements and model

Values of LDMC of sampled species ranged from 11.9% to 56.4%. LDMC values were lowest among a cohort of annual and perennial forbs, including *Gaillardia pulchella* (Walter) H. Rock, *Helianthus annuus* L. and *Vernonia baldwinii* Torr. (Fig. 1). LDMC values were highest among mid- to short-statured perennial grasses, including the C₄ grasses *Bouteloua curtipendula* (Michx.) Torr. and *Buchloe dactyloides* (Nutt.) Engelm. and C₃ grass *Nassella leucotricha* (Trin. & Rupr.) Barkworth. The intermediate range of LDMC values was populated by the annual grass *Bromus japonicus* Thumb. ex Murray, perennial forbs such as *Helianthus maximiliani* Schrad., and relatively tall-statured C₄ perennial grasses, including *Bothriochloa ischaemum* (L.) Keng, and *Panicum coloratum* L.

PLSR explained 73% and 62% of the variance in LDMC of canopies and individual leaves, respectively (Fig. 2). LDMC differences among canopies were associated with differences in canopy reflectance in violet (370–390 nm), blue (480–500 nm), red (640–675), red-edge to NIR (735–800 nm) and NIR (960–1010 nm) portions of the spectrum, as evidenced by standardized weightings of PLSR coefficients at these wavelengths (Fig. 2C). PLSR also identified blue, red-edge, and NIR bands as indicative of variation in LDMC of individual leaves. Leaf and canopy LDMC were positively correlated with reflectance in NIR (960–1000 nm) and blue wavebands (410 and 480–500 nm) and negatively correlated with reflectance in wavebands at the transition between the red-edge range and NIR plateau (~730–750) (Figs. 2C and 3). Patterns in these spectral ranges were expressed more consistently at the canopy than leaf levels. The LDMC of individual leaves was not correlated with either the ratio of reflectance at 900–970 nm,

indicative of leaf relative water content (Peñuelas et al. 1993; $P = 0.85$), or the NDVI of leaves ($P = 0.63$).

Plot-scale LDMC – relationship to community composition and NDVI

Change in the contributions of functional groups to community cover elicited change in community LDMC. Annual forb and grass species dominated in sampled plots (mean = 66% cover). Community LDMC was negatively correlated to fractional cover of annual forb species (Fig. 4A), as anticipated given the relatively low values of LDMC observed for the dominant forbs *G. pulchella* and *M. citiriodora* (Fig. 1). Cover of annual grasses in plots declined as cover of annual forbs increased (adj. $r^2 = 0.29$; $P < 0.0001$, $n = 128$; not shown). Residuals from the regression of annual grass cover versus annual forb cover were positively correlated with community LDMC, reflecting the higher LDMC values of leaves of dominant annual grasses [e.g. *B. tectorum* (23.2%), *Lolium perenne* (19.2%)] than forb species (Fig. 1). Residuals of annual grass cover explained 3% of variance in LDMC among plots in addition to that explained by annual forb cover (multiple regression; adj. $r^2 = 0.27$, $P < 0.0001$).

Change in community LDMC led to change in NDVI. High values of plot-scale NDVI in spring were associated with low values of community LDMC (Fig. 4B), implying that NDVI increased as dominance of annual forb species increased.

LDMC estimates at the spatial scale of the 7-m diameter patch were strongly correlated with LDMC averaged across the eight plots sampled per patch (Fig. S1). The slope of the regression relating the LDMC calculated from reflection of patches to the mean of LDMC values calculated from reflectance of the eight plots sampled per patch did not differ significantly from 1 [$(F_{1,28}) = 4.21$, $P > 0.05$]. The implication is that community LDMC at the patch scale was adequately predicted by the PLSR model developed using measurements at a smaller spatial scale.

Patch-scale LDMC – response to precipitation and effect on grassland NDVI

The spring peak in patch-scale NDVI varied among years because both community LDMC and the LDMC effect on NDVI differed among years in response to inter-annual variation in precipitation. Community LDMC was smallest on average during the wettest year (2016; 17.5%) and greatest during the driest year (2018; 29.2%) [October–April precipitation = 822, 624, 338 and 739 mm in 2016, 2017, 2018 and 2019, respectively]. The converse was true of patch NDVI (0.72 and 0.64, respectively). The community LDMC response to precipitation likely was associated

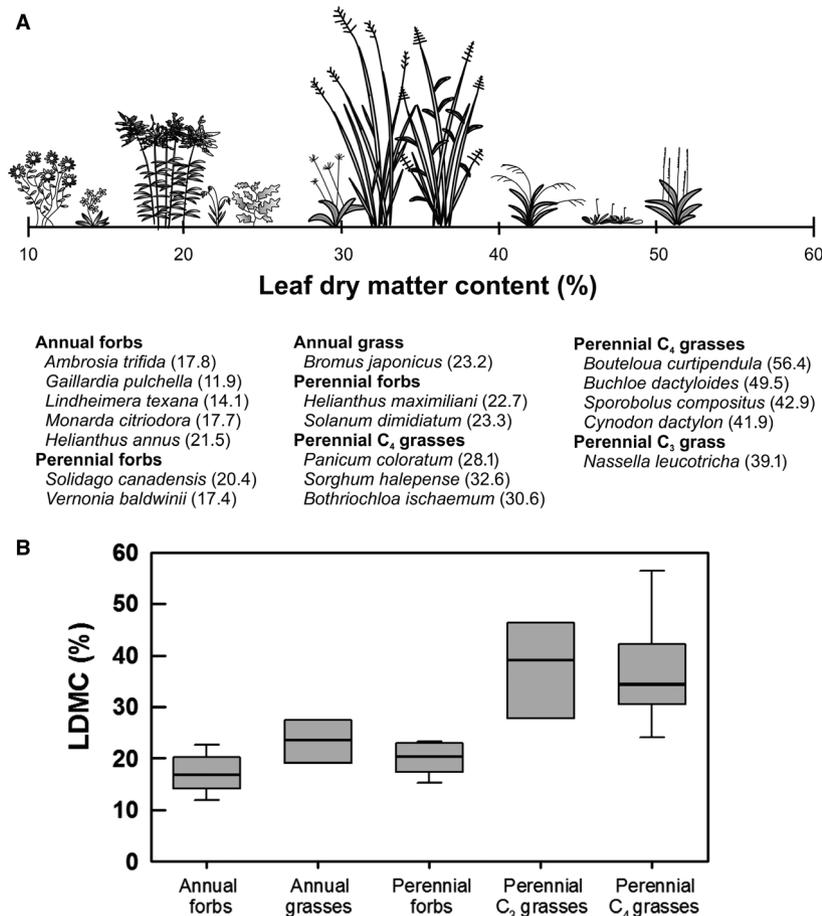


Figure 1. Leaf dry matter content (LDMC) differed by as much as a factor of 5 among grassland species sampled during spring (April–May). (A) The illustration depicts the shift in functional group composition and vegetation structure that typifies a shift in community LDMC in sampled grassland. Listed are selected species characterized by low (10–22.5%), medium (22.6–37.0%) and high (37.1–56%) values of LDMC (species LDMC values in parentheses). (B) Median values (bolded horizontal line) and the first and third quartiles (boxes) of the distribution of LDMC values among grassland species from five functional groups. Lines above and below boxes represent extreme values (whiskers). Box plots from which whiskers are absent represent three species only.

with shifts in species and functional group abundances. The median increase in patch LDMC from 2016 values was large among years (6.29%, 7.22% and 12.06% for years 2017, 2019 and 2018, respectively). However, greatest inter-annual change in LDMC occurred in patches in which LDMC values were lowest during the wet year of 2016 (Fig. 5). Aboveground biomass was a positive linear function of the maximum value of patch NDVI observed during spring 2016 (Fig. S2), implying that aboveground biomass during spring declined as precipitation decreased and community LDMC increased.

Patch NDVI also varied among years because of inter-annual differences in the LDMC effect on NDVI. NDVI was a negative linear function of patch LDMC measured during the spring peak in growth each year (Fig. 6). Community LDMC explained 60% of the variance in spring NDVI across years and patches on different soil types ($P < 0.0001$; $n = 416$), despite inter-annual variation in NDVI-LDMC regressions ($F_{(6,408)} = 20.6$, $P < 0.01$). Intercepts of NDVI-LDMC regressions for each year increased linearly as regression slopes became more negative (not shown), indicating that spring NDVI differed more among years for patches in which LDMC values were low than high. Slopes

and intercepts of NDVI-LDMC regressions correlated most strongly with precipitation during the month of March (adj. $r^2 = 0.79$ and 0.83 ; $P = 0.07$ and 0.06 , respectively).

NDVI-LDMC regressions differed between the two soil types across observations from 2016 through 2019 combined ($F_{(4,408)} = 30.6$, $P < 0.01$; not shown). The regression intercept was greater (0.87 and 0.85, respectively) and the regression slope was more negative (-0.0075 and -0.0069 , respectively) for the clay than silty clay soil. NDVI and, by inference, biomass production thus were slightly greater on average for the clay than silty clay soil when LDMC was low.

The magnitude of inter-annual change in spring NDVI depended more on the LDMC response to precipitation variation than on inter-annual change in the LDMC effect on NDVI. As estimated from the NDVI-LDMC regression fit to data from all patches and years combined, the maximum LDMC response to precipitation (decrease in LDMC from lowest to highest precipitation year; 12%) increased NDVI by approximately 0.08 (0.67–0.75 at mean LDMC = 21%). Inter-annual change in the LDMC effect on NDVI had a smaller impact on NDVI. The inter-annual shift in NDVI-LDMC regression relationships caused maximum

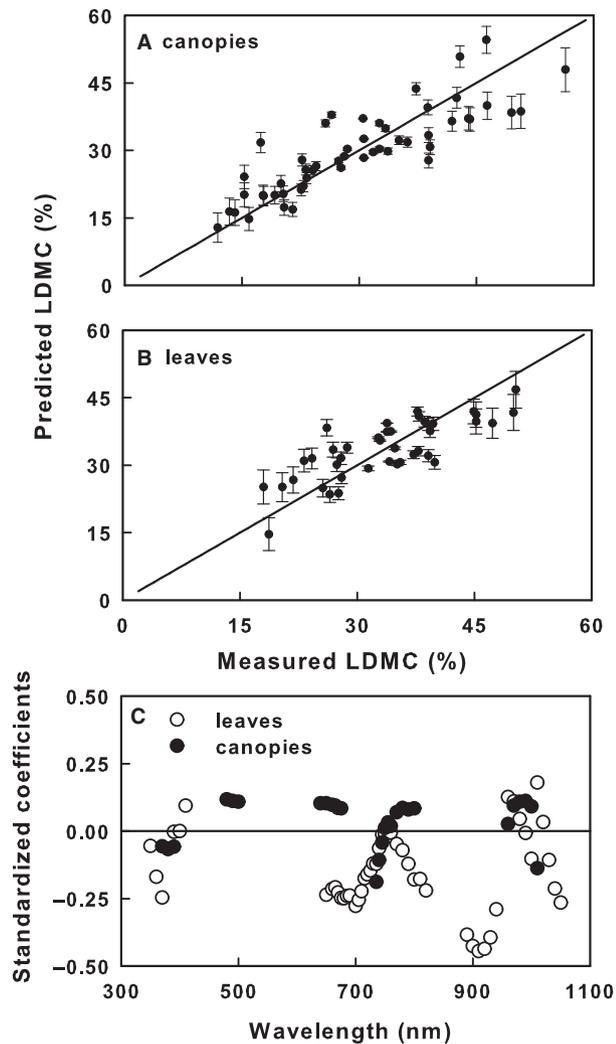


Figure 2. Relationships between measured values of LDMC and the LDMC calculated with PLSR using brightness normalized values of reflectance at the (A) canopy and (B) individual leaf levels. Bars for each data point denote the standard error of prediction. (C) Standardized weightings of regression coefficients from PLSR models for leaves and canopies. Lines in A and B represent the 1:1 relationship with measured LDMC. PLSR explained 73% and 62% of the variance in LDMC of canopies (3 latent variables; 28 wavebands; PRESS = 0.64; RMSE = 5.69; $n = 52$) and individual leaves (5 latent variables; 50 wavebands; PRESS = 0.86; RMSE = 5.80; $n = 41$), respectively.

change in NDVI of 0.06 (0.73–0.79) at LDMC = 15% versus change of 0.03 (0.58–0.61) at LDMC = 35%.

Discussion

Grassland LDMC was well-described by a regression (PLSR) model using canopy reflectance in red edge and NIR wavebands. Modeled LDMC varied by a factor of 4 among 76-cm diameter plots of restored grassland in

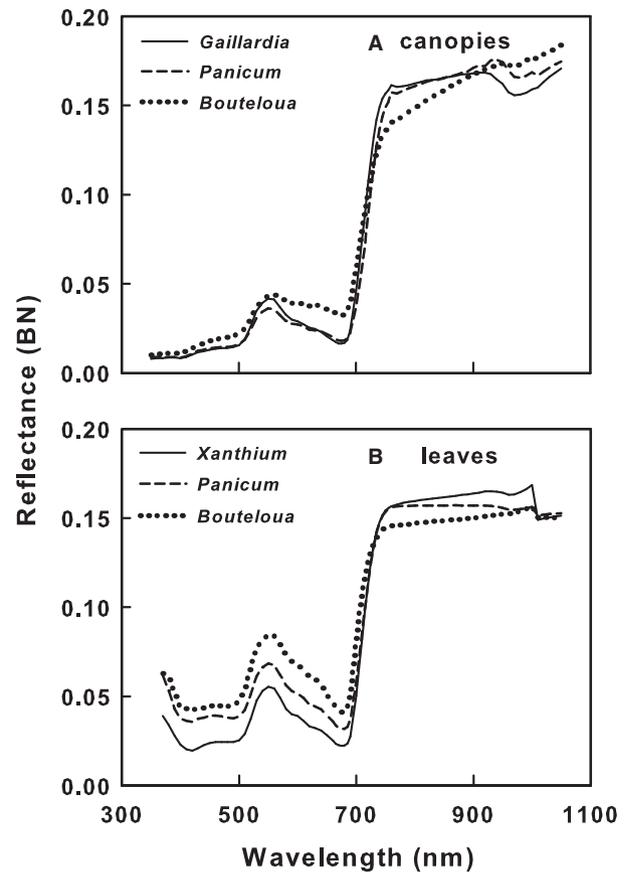


Figure 3. Brightness normalized (BN) values of reflectance as a function of wavelength for selected (A) canopies and (B) individual leaves of species that differed in LDMC. Differences in leaf and canopy LDMC were associated most consistently with reflectance differences in wavebands in the transition zone between the red-edge and NIR plateau (~730–750) and NIR (960–1000 nm; see Fig. 2C). Illustrated is reflectance from (A) canopies of *Gaillardia pulchella*, *Panicum coloratum* and *Bouteloua curtipendula* [LDMC (%) = 11.9, 28.1 and 44.0, respectively] and individual leaves of *Xanthium strumarium*, *Panicum coloratum* and *Bouteloua curtipendula* [LDMC (%) = 18.0, 32.7 and 50.3, respectively].

spring, reflective of variation in relative abundances of functional groups of species. Community LDMC was high in plots dominated by annual forb species and decreased linearly as forb abundance declined. The compositional differences in plant communities that led to variation in LDMC were linked to inter-annual change in grassland biomass production, as inferred from change in NDVI, at the scale of 7-m diameter patches. NDVI in spring declined linearly as community LDMC of patches increased. Decreased precipitation reduced spring NDVI both by increasing community LDMC (LDMC response) and reducing the slope of the NDVI-LDMC relationship (LDMC effect on NDVI). Our results confirm a strong correlation between community LDMC and both community composition and

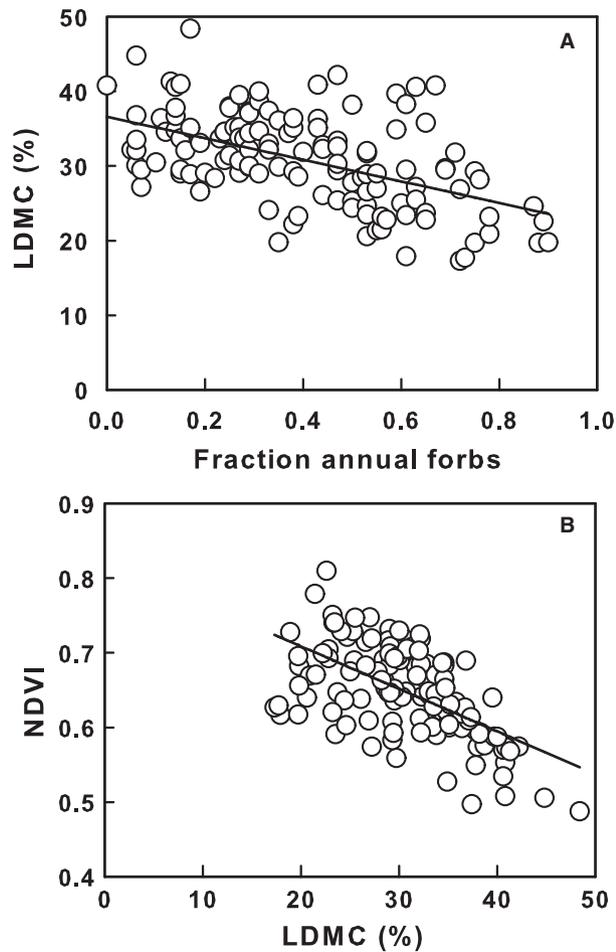


Figure 4. Relationship between (A) community LDMC and fractional cover of annual forb species and between (B) NDVI and community LDMC for 76-cm diameter plots sampled in spring. LDMC was calculated from brightness normalized values of canopy reflectance using a calibrated PLSR model. Lines were fit using linear regression (A; adj. $r^2 = 0.24$, $P < 0.0001$; B; adj. $r^2 = 0.35$, $P < 0.0001$, $n = 128$). Note that the y-axis scale in (B) does not include the origin.

functioning and demonstrate the utility of spectral estimates of LDMC for discerning shifts in grassland composition and predicting consequences for production.

A regression model developed using reflectance from single-species stands described spatial variation in community LDMC that was consistent with differences in the functional group composition of grassland. Importantly, the wavebands most indicative of variation in community LDMC matched those that described variation in leaf-level LDMC. Wavebands diagnostic of LDMC were concentrated in the red-edge and NIR regions of the spectrum, the latter including the water absorption peak at 970 nm. Others have demonstrated an association between dry matter and reflectance bands in these spectral regions (Wang et al. 2011; Chadwick and Asner 2016; Ely

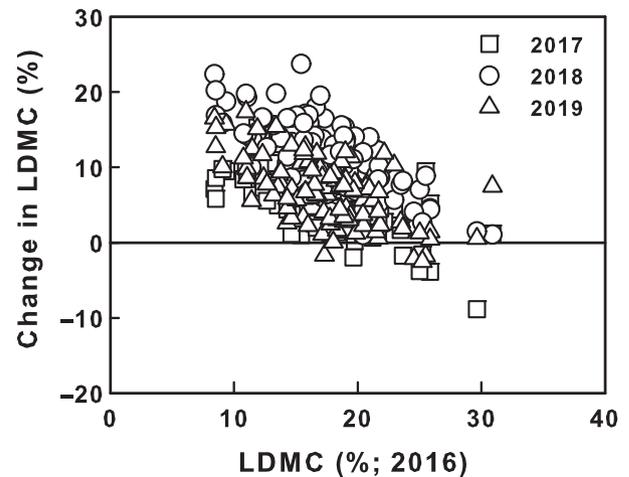


Figure 5. The change in community LDMC of 7-m diameter patches of restored grassland between years 2, 3 and 4 (2017–2019) of measurements and year 1 (2016; e.g. LDMC in 2017 minus LDMC in 2016) plotted versus patch LDMC in 2016.

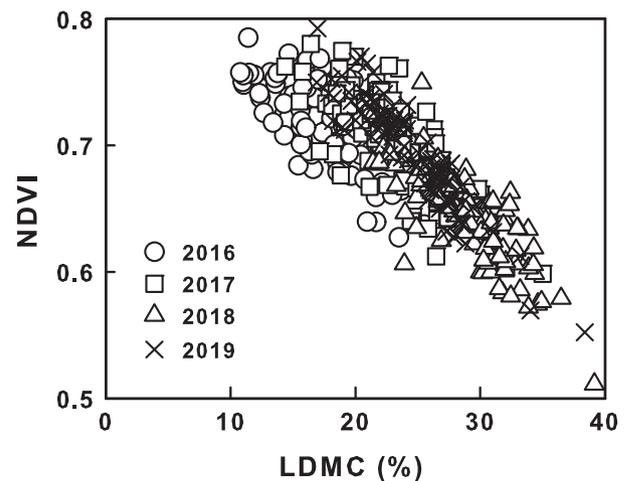


Figure 6. Relationship between the spring maximum in NDVI of 7-m diameter patches in restored grassland and the spring minimum in community LDMC during each of 4 years (2016–2019, $n = 104$). LDMC was calculated from brightness normalized values of canopy reflectance using a calibrated PLSR model.

et al. 2019). Reflectance at 970 nm was positively correlated to LDMC at both the individual leaf and community scales. This correlation implies that high LDMC was associated with low plant water content, as should be expected. Conversely, LDMC was negatively correlated with reflectance in the red edge region. Wang et al. (2011) found that red-edge reflectance was high in leaves with reduced mass per unit of area and declined as dry matter increased. Our observation that LDMC and red-edge reflectance were negatively correlated thus is consistent with the interpretation that reflectance varied with

LDMC at least partly because samples differed in dry matter.

Patch-scale NDVI of grassland was a strong negative function of community LDMC. We infer that spring NDVI was greatest in patches dominated by annual forb species with low LDMC and smallest in patches dominated by short-statured perennial grasses with high LDMC. Our results are consistent with the negative effect of high LDMC on grassland biomass production or growth rate reported from other ecosystems (Garnier et al. 2004; Duru et al. 2009). Contrary to expectation, however, the LDMC effect on grassland NDVI during spring was correlated with precipitation during a single month, rather than with variation in the October–April sum of precipitation that elicited change in LDMC. NDVI differed more among years for patches in which LDMC values were low than high. A negative relationship between biomass variability and community LDMC was demonstrated previously (Polley et al. 2013).

Grassland NDVI varied among years largely because LDMC varied in response to inter-annual change in precipitation. The dynamic nature of grassland LDMC is well established. Community LDMC has been shown to shift with fertility, temperature and management activities, including differences in grazing intensity (Duru et al. 2010). Less information is known of the extent to which the LDMC effect on production (here, the NDVI–LDMC relationship) varies with change in the environment or management. The LDMC effect on spring NDVI of restored grassland was, by comparison to the LDMC response, conserved. The opposite was observed for relationships between production and community specific leaf area (SLA) of stands of perennial grass and forb species (Polley and Wilsey 2018). Inter-annual change in above-ground production (ANPP) of perennials resulted more from change in the trait effect on production (ANPP–SLA relationship) than trait response to precipitation. Temperature or other constraints on the growth of warm-season species apparently limited variation in the LDMC effect on NDVI of restored grassland during spring.

Our results demonstrate that grassland LDMC can be modeled using airborne measurements of canopy reflectance in visible and NIR wavebands. Modeled LDMC provided insight into effects of inter-annual variation in precipitation on grassland NDVI. NDVI during spring increased as precipitation increased largely because greater precipitation favored productive species with low values of LDMC.

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of Agriculture. USDA is an equal opportunity provider and employer.

Data Accessibility

Spectral data will be deposited in EcoSIS.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Relationship between community LDMC of 7-m diameter patches and the mean of LDMC values calculated for 8, 76-cm diameter plots per patch. LDMC was calculated with PLSR using brightness normalized values of canopy reflectance collected at each spatial scale. The line was fit using linear regression (adj. $r^2 = 0.65$; $P < 0.0001$; $n = 16$). The slope of the linear regression (0.72) does not differ significantly ($P > 0.05$) from the value of 1 expected if the PLSR model predicts LDMC equally well at the patch and plot scales.

Figure S2. Relationship between aboveground biomass and NDVI during spring for 7-m diameter patches in restored grassland. The line was fit using linear regression (adj. $r^2 = 0.54$, $P < 0.0001$; $n = 32$). Note that x- and y-axis scales do not include the origin.

Table S1. Leaf dry matter content (LDMC) of single leaves on which spectral reflectance was measured ($n = 41$ samples). Measurements were used to develop a partial least squares regression model relating LDMC to leaf reflectance. Replicate samples for a given species are distinguished by the number in parentheses following the species name. Sampled species segregate into four functional groups.