USING IMAGING SPECTROSCOPY TO ESTIMATE INTEGRATED MEASURES OF FORAGE QUALITY FOR BROWSING HERBIVORES

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1. INTRODUCTION

Concentrations of nutrients and chemical defenses in plant foliage are both genetically and environmentally determined (Andrew et al. 2007; Ollinger et al. 2002). This results in a patchy distribution of forage quality within a landscape, even if it appears homogenous in terms of species composition and density of cover (DeGabriel et al. 2009; Mutanga et al. 2005). Studies of animal foraging have found significant relationships between individual foraging decisions and plant nutrients and plant chemical defenses (Marsh et al. 2003a; Provenza et al. 2003). Likewise, herbivore distributions have been linked to variations in the chemical quality of forage (Ball et al. 2000; Pausas et al. 1995). The ability to map certain chemicals in plant foliage on a landscape-scale may provide an indication of habitat quality for some herbivorous species (Leyequien et al. 2007). In addition, landscape-scale measurements of plant biochemistry can provide important information about ecosystem processes and functioning (Asner and Vitousek 2005; Smith et al. 2002).

Until recently, assessing plant chemistry on a landscape-scale has been impractical because it required sampling thousands of leaves in the field for lengthy laboratory analyses. Recent technological advances in near-infrared spectrometry and hyperspectral remote sensing are opening the door to the rapid assessment of leaf chemical composition in the lab and across whole forest canopies (for reviews see, Kokaly et al. 2009; Majeke et al. 2008). Imaging spectroscopy builds upon the extensive laboratory near-infrared spectrometry research that has identified strong relationships between the absorption of electromagnetic radiation and various chemical constituents (Curran 1989; Ebbers et al. 2002). Molecular vibrations resulting from the rotation, bending and stretching of chemical bonds absorb electromagnetic radiation at frequencies that correspond to their energy state and create harmonics and overtones in the near-infrared (NIR) and shortwave infrared (SWIR) regions of the electromagnetic spectrum (Kokaly et al. 2009). Variations in reflectance at wavelengths that correspond to specific molecular interactions can be used to identify and quantify the chemical composition of materials based on high resolution spectral data.

Imaging spectroscopy has received considerable attention as a potential tool to estimate forage quality on a landscape scale (for a review see Leyequien et al. 2007). Most research in this area has focused on the ability to estimate foliar concentrations of nitrogen (N) because N is believed to be a limiting nutrient for many herbivorous species (Kavanagh and Lambert 1990, White 1993). However, the total quantity of foliar N does not necessarily reflect the amount of N that can be digested and utilized by herbivores. Studies of herbivore foraging have suggested that more attention should be directed towards integrated measures of forage quality (e.g., nitrogen availability) rather than individual nutrients (Foley and Moore 2005; McArt et al. 2009). This lead Degabriel et al. (2008) to develop an *in vitro* assay to measure forage quality that integrates the effects of fiber and condensed tannins (CTs) on the amount of N that is available for digestion (AvailN). CTs are a common plant secondary metabolite (PSM) that can bind to nitrogenous compounds in plant tissues and further reduce the digestibility of plant proteins (Hagerman et al. 1992). CTs also can interfere with the ability of animals to detoxify other PSMs (Min et al 2003). High levels of CTs can reduce forage intake by herbivores (Marsh et al. 2003b; Robbins et al. 1987). For the many herbivorous species that are sensitive to CTs, AvailN may be a more meaningful measure of forage quality than total foliar N (DeGabriel et al. 2008; Foley and Moore 2005).

The link between concentrations of N and specific absorption features in the electromagnetic spectrum are well established and numerous studies have attempted to estimate foliar N from remote sensing data with varying success (for a review see, Majeke et al. 2008). However, using imaging spectroscopy to estimate N availability for herbivores would be a significant advance. In addition, the majority of research into quantifying foliar biochemicals with remote sensing data has focused on homogenous, single species canopies or aggregated, plot-level measurements (for examples see, Coops et al. 2002; Huang et al. 2004; Smith et al. 2003, but for exception see Huber et al. 2008). We collected hyperspectral remote sensing data (HyMap) over a native *Eucalyptus* forest in southeastern Australia. Using a combination of laboratory near infrared spectrophotometry, a recently developed *in vitro* assay for AvailN and two powerful spectral transformation methods, continuum-removal and derivative analysis, we developed linear regression models to scale concentrations of total foliar N, AvailN and digestible dry matter (DDM) from leaf to canopy-level. These three foliar constituents have the potential to provide a useful measure of forage quality for a wide-range of herbivorous species and are known to play a role in forage choice and habitat quality for several arboreal marsupial folivores indigenous to our study area (DeGabriel et al. 2009; McIlwee et al. 2001). The model estimates achieved R2-values between 0.55 and 0.64 for AvailN, 0.54-0.60 for N and 0.75-0.78 for DDM. The models selected wavebands that largely correlate to known absorption features. This and the large contribution of a small number of wavebands suggest that it may be possible to develop prediction algorithms based on a few wavelengths that could be extrapolated to other landscape types. The ability to model integrated measures of forage quality on a landscape-scale would increase our understanding of plant-animal interactions and could greatly improve the management and conservation of many herbivorous species.

Table 1. Results from modeling (MPLS, step-up and stepwise regression with cross-validation) the relationship between the foliar concentrations of nitrogen (N; % dry matter (DM)), available nitrogen (AvailN; % DM) and digestible dry matter (DDM; g/g DM) and the spectral characteristics of *Eucalyptus* canopies collected with an airborne hyperspectral sensor (HyMap).

Constituent	Math treatment	Statistical method	SEC	SECV	R^2	Selected wavelengths* or number of terms (MPLS only)
N	2,2,2,1	MPLS	0.9	0.11	0.54	2 terms
N	2,1,1,2	Step-up	0.10	0.10	0.60	1662, 1785, 1476, 1419, 624, 908
N	2,1,1,2	Stepwise	0.10	0.10	0.58	624, 908, 1785, 1662, 1419
AvailN	2,4,4,1	MPLS	0.15	0.18	0.55	3 terms
AvailN	2,1,1,1	Step-up	0.16	0.16	0.64	1675, 1330, 2174, 475, 810, 1971
AvailN	2,1,1,1	Stepwise	0.15	0.15	0.64	824, 475, 2174, 1330, 1675, 1462
DDM	2,4,4,1	MPLS	0.05	0.06	0.75	4 terms
DDM	1,1,1,1	Step-up	0.06	0.07	0.77	1675, 954, 739, 652 , 594, 2297
DDM	1,4,4,1	Stepwise	0.06	0.06	0.78	1558, 969, 652, 594, 1637

Models are based on the maximum spectra of pixels collected from individual tree canopies. Continuum-removal analysis and standard normal variate scatter correction and detrending (SNV-detrend) were applied to the full spectrum of all samples before modeling. Math treatment refers to the Savitzy-Golay derivative based spectral smoothing and includes the derivatives and the number of data points across which the smoothing functions were calculated (e.g., 2,4,4,1 indicates that the second derivative (2) was calculated with a primary smoothing of 4 nm (4) across a gap size of 4nm (4) and no secondary smoothing (1)); SEC is standard error and SECV is standard error of cross-validation predictions. The degree of correlation between predicted and analyzed values is indicated by the R^2-value. *Wavelengths are listed in the order of selection.

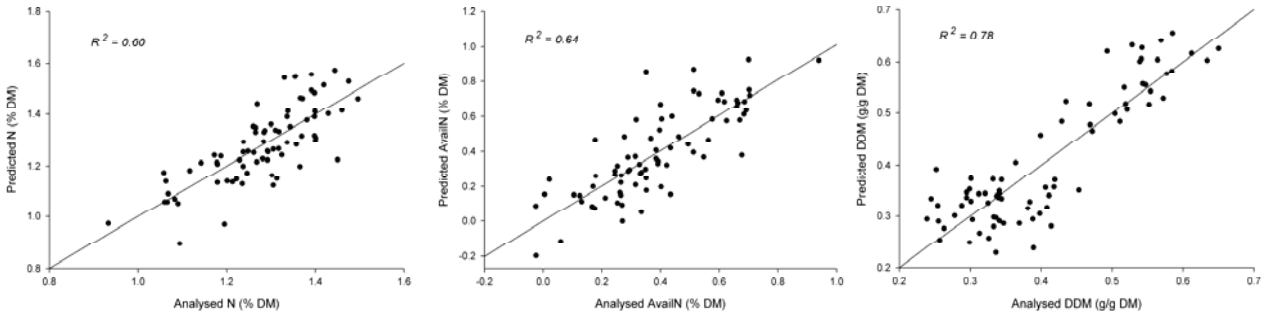

Fig.1. Predicted vs. analyzed foliar concentrations of nitrogen (N; % dry matter (DM)), available nitrogen (AvailN; % DM) and digestible dry matter (DDM; g/g DM) using step-up (for N) and stepwise (for AvailN and DDM) regression models applied to the transformed HyMap maximum spectra. The degree of correlation between the predicted and analyzed values is provided by R^2.

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