THE USE OF HIGH SPECTRAL RESOLUTION REMOTE SENSING TO DETERMINE LEAF PALATABILITY OF EUCALYPT TREES FOR FOLIVOROUS MARSUPIALS.

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ABSTRACT

In this study we assess the feasibility of remotely measuring canopy biochemistry, and thus the potential for conducting large-scale mapping of habitat quality. A number of studies have found nutrient composition of eucalypt foliage to be a major determinant of the distribution of folivorous marsupials. More recently it has been demonstrated that a specific group of secondary plant chemicals, the diformylphloroglucinols (DFPs), are the most important feeding deterrents, and are thus vital determinants of habitat quality. We report on the use of imaging spectroscopy to attempt to identify one such DFP, sideroxylonal-A, in the foliage of *Eucalyptus melliodora*, one of the few eucalypt species browsed by folivorous marsupials. Reflectance spectra were obtained for freeze-dried, ground leaves using near infrared spectroscopy (NIRS) and for both oven-dried and fresh whole leaves using a laboratory-based (FieldSpec) spectroradiometer. Modified partial least squares (MPLS) regression was used to develop calibration equations for sideroxylonal-A concentration based on the reflectance spectra transformed as both the first and second difference of absorbance (Log 1/R). The predictive ability of the calibration equations was assessed using the standard error of calibration statistic (SECV). Coefficients of determination (r^2) were highest for the ground leaf spectra (0.98), followed by the fresh leaf and dry leaf spectra (0.94 and 0.87, respectively). When applied to independent validation sub-sets, sideroxylonal-A was most accurately predicted from the ground leaf spectra ($r^2 = 0.94$), followed by the dry leaf and fresh leaf spectra (0.72 and 0.53, respectively). Two spectral regions, centred on 674 nm and 1394 nm, were found to be highly correlated with sideroxylonal-A concentration for each of the three spectral data sets studied. Results from this study suggest that calibration equations derived from modified partial least squares regression may be used to predict sideroxylonal-A concentration, and hence leaf palatability, of *E.melliodora* trees, thereby indicating that the remote estimation of habitat quality of eucalypt forests for marsupial folivores is feasible.

1   INTRODUCTION

The Australian environment is characterised by poor quality soils and high levels of solar radiation. This disproportionate balance of soil nutrients to carbon availability (via photosynthesis) allows plants a high investment in carbon-based secondary metabolites, as exemplified by Eucalyptus, the tree genus which dominates most Australian forests (Landsberg and Cork, 1997). As a result, the foliage of these trees is often a poor quality food resource to the extent that large portions of Australian forests do not support viable populations of leaf-eating mammals (Braithwaite *et al.*, 1983; Cork and Catling, 1996). Only four mammalian species, all marsupials, have digestive and metabolic adaptations that permit them to eat eucalypt foliage. These are the common ringtail possum (*Pseudocheirus peregrinus*), the greater glider (*Petauroides volans*), the koala (*Phascolarctos cinereus*), and, to a lesser extent, the common

brushtail possum (*Trichosurus vulpecula*). Clearing has removed much of the forest from the most productive soils, and contemporary forest management activities remain a source of conflict between conservation organisations and timber/farming industries (National Forest Inventory, 1998). Identification of the habitat requirements for these arboreal, folivorous marsupials has therefore become an important priority among forest ecologists in Australia.

Pausas *et al* (1995) modelled a number of factors (e.g. foliage and soil nutrients, site characteristics, forest structure) thought to explain the distribution of folivorous marsupials in eucalypt forests, and concluded that the main factor predicting their occurrence is leaf nutrient quality. These results are consistent with other studies that have shown leaf nutrient quality to be a major determinant of the distribution of folivorous marsupials in eucalypt forests (Braithwaite *et al.*, 1983, 1984, Norton, 1987, Kavanagh and Lambert, 1990, Cork, 1992).

Eucalypt foliage presents particular nutritional challenges through having low concentrations of nutrients, high concentrations of components that interfere with digestion (e.g. lignin and tannins) and a range of potentially toxic allelochemicals, mainly carbon-based chemical defenses such as phenolics and terpenoids (essential oils), that deter herbivores because of their taste or post-ingestive consequences (Fox and Macauley, 1977, Cork and Foley, 1991, 1997, Cork, 1996). Phenolics may comprise up to 40% of foliar dry matter in eucalypts, much higher than in other forests in the world (Fox and Macauley, 1977, Cork, 1996).

Early studies of PSM-herbivore interactions focused on non-absorbable phenolics, such as tannins, because they are ubiquitous and because it was believed that they interfered with digestive processes by binding protein in the gastrointestinal tract (McArthur and Sanson, 1993). However, it is becoming increasingly evident that the role of tannins as reducers of protein digestibility has been over-emphasised (Foley *et al.*, 1999, Pass and Foley, 2000).

Recent advances in the chemical identification of *Eucalyptus* PSMs have resulted in better correlative relationships between feeding and individual absorbable phenolic constituents of eucalypt foliage (Lawler *et al.*, 2000). In particular, a newly discovered group of PSMs, the diformylphloroglucinol compounds (DFPs), have been found to play an important role in deterring feeding by marsupial folivores (Lawler *et al.*, 1998a,b, 1999, 2000, Pass *et al.*, 1998). Lawler *et al.* (1998a) developed a method to quantify sideroxylonals, a subset of the DFPs, and have shown that in *Eucalyptus* species where sideroxylonal is the predominant DFP, it explains the majority of variation in feeding by marsupial folivores among individual trees (Lawler *et al.*, 2000).

Near infrared spectroscopy (NIRS) has been found to be a useful tool for modelling aspects of the intake and digestion of forages containing plant secondary metabolites (Foley *et al.*, 1998). Examination of spectral characteristics obtained with NIRS has revealed strong relationships between functional groups of PSMs and specific wavelengths (Windham *et al.,* 1988, McClure and Williamson, 1988, Clark *et al.,*1987, Roberts *et al.,* 1993, Mika *et al.,* 1997). By applying an NIRS-based model to feeding by common ringtail possums, fed three species of *Eucalyptus* foliage, Lawler *et al.* (2000) explained more than 80% of the variation in foliage intake. This matched the explanatory power of a detailed and time-consuming investigation of the secondary chemistry of the plants.

Traditional methods for assessing foliar chemistry involve the collection of field samples, their drying and grinding, followed by laboratory analyses. These measurements are costly and time consuming, and impractical to apply over large areas. By sensing variations in solar energy absorptance caused by the presence of foliar biochemical compounds, near infrared spectroscopy (NIRS) can significantly reduce the time spent on laboratory analyses. Examination of spectral characteristics obtained with NIRS has revealed strong relationships between functional groups of PSMs and specific wavelengths (Windham *et al.,* 1988, McClure and Williamson, 1988, Clark *et al.,*1987, Roberts *et al.,* 1993, Mika *et al.,* 1997). It has been also found to be a useful tool for modelling aspects of the intake and digestion of forages containing PSMs. By applying an NIRS-based model to feeding by common ringtail possums fed three species of *Eucalyptus* foliage, Lawler *et al.* (2000) explained more than 80% of the variation in foliage intake. This matched the explanatory power of a detailed and time-consuming investigation of the secondary chemistry of the plants.

In this study we report on the use of imaging spectroscopy to attempt to measure leaf palatability through the estimation of sideroxylonal-A concentration in the foliage of individual *Eucalyptus melliodora*. This will give an indication of the potential for conducting regional-scale mapping of tree palatability/habitat quality through the use of airborne/spaceborne imaging. Reflectance spectra obtained in the laboratory using whole, fresh leaf samples are analysed to establish whether calibration equations derived from the radiometric properties of *E. melliodora* foliage can be used to predict sideroxylonal-A concentration, and the results are compared with those obtained using whole, dry leaf samples and freeze-dried, ground leaf material.

2 METHODS

Leaf samples were collected in June 1998 and April 1999 from 85 *E.melliodora* growing in open woodland approximately 20km east of Canberra. All samples were of fully-expanded adult foliage from the mid to upper canopy. An Analytical Spectral Devices (ASD) FieldSpec FR spectroradiometer, which senses in the spectral range 350 to

2500nm with a spectral resolution of between 3 and 10nm, was used in the laboratory to measure spectral reflectance of both the intact fresh leaf samples and oven-dried leaves (70°C for 48 hours) from each tree.

Reflectance measurements of the fresh leaf samples were made within 4 hours of the leaves being detached. Experiments on signal degradation with time showed that there was no change in the spectral reflectance of the leaves within the first 4 hours after detachment. A constant source of illumination was provided by a modified Makita high intensity reflectance probe. Multiple leaf layers were used to ensure reflectance saturation. Average reflectance (R) was calculated from ten spectral recordings per tree, and converted to log (1/R), a form analogous to absorbance and, assuming Beer's Law, approximately linear with concentration. This procedure was repeated for sub-samples of oven-dried leaves from each tree. Near infrared spectroscopy (NIRS) was used to collect spectra from a sub-sample of freeze-dried, ground leaf material from each tree.

Leaf sideroylonal-A concentrations (mg per g of leaf dry matter) were determined on freeze-dried leaf material using a modified procedure of that described by Lawler *et al.* (2000). Briefly, 1.5 g of dried, ground leaf was extracted for 13 h with 100 mL of 8:2 light petroleum spirit (40-60°C BP):acetone in a soxhlet apparatus. The solvent was removed by rotary evaporation at 50°C and the resulting crude extract transferred quantitatively into a preweighed vial with five 3 mL aliqots of 8:2 dichloromethane:methanol. The vial was reweighed after drying under air for 48 h. A known mass of the crude extract (11 ± 1 mg) was dissolved in exactly 10mL of HPLC running solvent (95% methanol, 4.9% water, 0.1% TFA). After filtering (0.45 µm), 15 µL was injected onto a reverse phase C-18 column (YMC J'sphere ODS-L80; 150 x 4.6mm ID) with the above running solution pumping at 1.0 mL per minute. Sideroxylonal-A elutes at about 4.1 minutes and was quantified with a standard curve.

Both first and second derivatives (multiple order differentiation of the Log 1/R data) were calculated. Derivatization is effective in reducing errors from baseline shifts in the data and interfering absorptions (Dixit and Ram, 1985). A number of derivative math treatments were evaluated, expressed as D, G, S1, S2, where D = the derivative number (either first or second), G = the gap between points used to calculate the difference (4 or 8), and S1 and S2 the number of data points used to smooth the data (4, 6 or 8 and 1, respectively). The first derivative minimises the signal due to a strong but gradually varying absorber, in this case water, in favour of a weak but rapidly varying absorber (Wessman, 1990), as might be expected for sideroxylonal-A. The gap size and amount of smoothing used to make the transformation will affect the number of apparent absorption peaks

A modified partial least squares (MPLS) regression technique was used to regress spectral data against the corresponding sideroxylonal-A concentrations. This method is superior to stepwise multiple linear regression for determination of leaf chemistry by NIRS, and is less likely to result in overfitting (Shenk and Westerhaus, 1991, Bolster *et al.*, 1996). PLS reduces the spectral data to a few combinations of the absorbance values that not only explain much of the spectral information but also relate to the sample reference (ie sideroxylonal-A) values. We used cross validation to estimate the optimal number of terms for the calibration, in which the population is arbitrarily divided into a small number of groups, and a prediction is made of the values for one group based on calibrations developed from the remaining groups. In turn, predictions were made for all groups with the average of predictions for all groups (Shenk and Westerhaus, 1993). Although this means the requirement to maintain separate validation and calibration sets is no longer strictly necessary, we have nonetheless done so as an additional means of verification. Of the 85 samples, 60 were randomly selected for calibration (for both dry and fresh leaf data-sets) and 25 retained as validation samples. Fifty samples are recommended as the minimum for calibration, although a higher percentage should yield more accurate predicted values (Shenk *et al.,* 1978). The calibration data-set was used to establish the coefficients in the regression equations. The resulting calibration equations were then used to predict the sideroxylonal concentrations of the validation data sets. Validation samples were combined with the calibration set to derive the final regression equations.

The predictive ability of the calibration equations was assessed using the coefficients of multiple determination (r^2) and, foremost, the standard error of calibration statistic (SECV), which is based on an iterative calibration-validation algorithm. The equation with the lowest SECV and highest r^2 is selected as the best calibration (Mark and Workman, 1991).

Scatter is a nonlinear function that can distort the relationship between the spectrum and the reference, although a number of scatter correction techniques are available that minimize the variations of scattering due to variable particle-size, and account for variation in baseline shift and curvilinearity (Barnes *et al.*, 1989). Four methods of scatter correction were compared: using a Standard Normal Variate (SNV) and de-trending transformation (evaluated together and separately), a multiplicative scatter correction (MSC), and using raw spectra only (ie. no scatter correction). Outliers were assessed based on t-statistics and their standardized Mahalanobis (H) distance from the average spectrum of the file (Mark and Tunnell, 1985) and if neccesary, eliminated . These were assumed to be the result of mistakes, either in the spectra or in the chemistry measurement.

3   RESULTS

The 'best' predictive equations obtained for the first and second derivative transformations of the Log 1/R data for each of the three sets of leaf spectral measurements are reported in Table 1, ((listing math treatment, scatter correction, r^2, SECV, and the number of samples used in the equation)).

Spectra below 500 nm were eliminated from the FieldSpec spectrometer measurements prior to analysis, because of inconsistent readings encountered in this spectral region. This prevented subsequent comparisons across data sets for these wavelengths.

3.1   Freeze-dried, ground leaf material

The regression models using the first and second derivative transformations of the Log 1/R data sets predicted the validation data sets with coefficients of determination (r^2) of 0.94 and 0.89, respectively (Fig 1a,b).

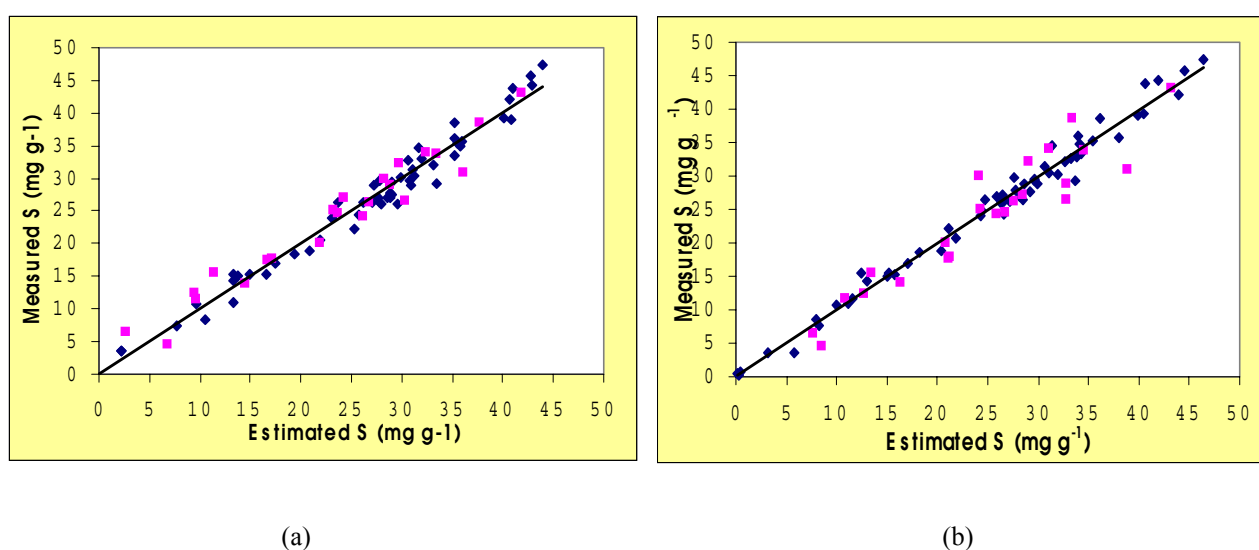(a)   (b)

Fig 1. Plot of measured versus predicted sideroxylonal-A (S), using calibration regression equations generated for freeze-dried, ground leaf data set, for a) first derivative and b) second derivative Log 1/R data. The validation data is represented by lighter squares.

The 'best' calibration regressions for the first and second derivative transformations gave similar results in terms of r^2 and SECV (see Table 1). The regression equations of the combined calibration and validation data sets show that while both have r^2 of 0.98, the first derivative transformation was superior to the second through having a lower SECV.

Fig 2 depicts the correlation between first derivative transformed NIRS absorbance and the sideroxylonal-A concentration of *E. melliodora* samples. The three major correlation peaks for the first derivative transformation of the Log 1/R data occur at a broad band of wavelengths centred on 856 nm, a narrower band centred on 1394 nm, and a third peaking at 1902 nm. Other correlation peaks occur at wavelength bands centred on 450, 568, 618, 674, 1222, 2320, 2406 and 2478 nm.

The three major correlation peaks for the second derivative transformation of the Log 1/R data occur at 1156 nm, 1334 nm and 1910 nm. Other notable correlation peaks (r > 0.57) occur at 486, 574, 626, 682, 886, 916, 1156, 1240, 1334, 1404, 1458, 1910, 2136, and 2244 nm.

Table 1. Summary of results from modelling the relationship between spectral characteristics of E.melliodora foliage and the foliar concentration of sideroxylonal-A.

	r^2	SECV	Mathematical treatment	Scatter correction	N
Freeze-dried ground leaf					
All samples	0.98	2.53	1441	SNV	81
	0.98	3.04	2441	SNV/Detrend	83
Calibration set	0.98	3.12	2441	SNV/Detrend	58
	0.97	3.22	1441	SNV	59
Whole oven-dried leaf					
All samples	0.85	5.98	1881	Detrend	82
	0.87	6.86	2881	SNV/Detrend	81
Calibration set	0.82	6.64	1881	SNV/Detrend	59
	0.89	6.90	2881	SNV/Detrend	59
Whole fresh leaf					
All samples	0.91	5.22	1881	SNV	81
	0.94.	6.06	2881	SNV/Detrend	85
Calibration set	0.91	5.71	1881	SNV/Detrend	59
	0.94	6.13	2881	SNV/Detrend	60

Note: "Mathematical treatment" refers to the derivatives and range of data points over which the derivative and smoothing functions were calculated. Thus 1,4,4,1 refers to first derivative, a gap of 4 nm (ASD spectrometer) or 8 nm (near infrared spectrometer, which records reflectance every 2 nm), and a smoothing over 4 data points.
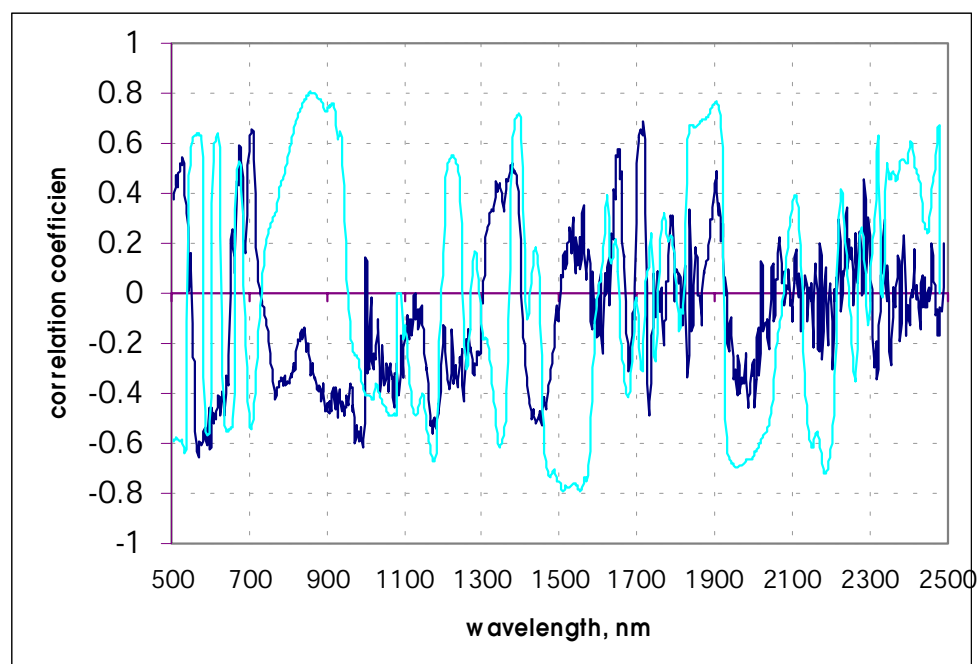

Fig. 2. Correlogram of sideroxylonal-A concentration by wavelength for freeze-dried ground leaf material (lighter line), compared with correlations for fresh leaf (darker line).

3.2   Whole dry leaves

The regression model using the first derivative transformation of the validation data set resulted in a more reliable prediction ($r^2 = 0.72$; Fig3a) than that obtained using the second derivative transformation ($r^2 = 0.58$; Fig3b).

The first derivative transformation of both the calibration and combined calibration and validation data had the lowest SECVs (6.64 and 5.98 respectively), with corresponding coefficients of determination of 0.82 and 0.85 (Table 1).

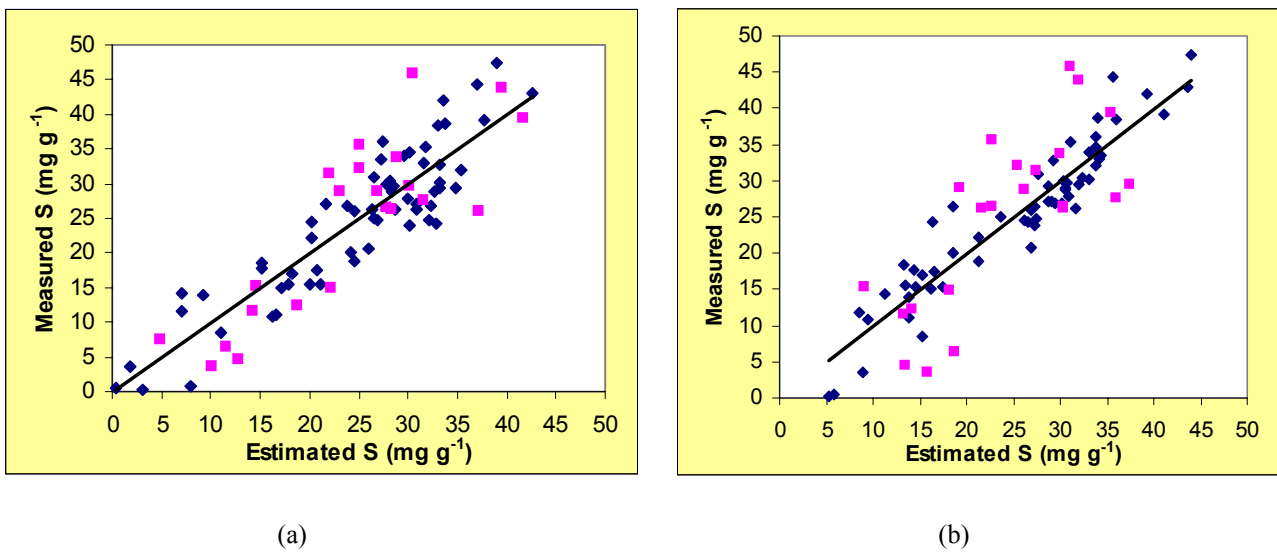(a)   (b)

Fig 3. Plot of measured versus predicted sideroxylonal-A (S), using calibration regression equations generated for whole, oven-dried leaf data set, for a) first derivative and b) second derivative Log 1/R data. Validation data are represented by lighter squares.

The correlation between first derivative transformed spectrometer absorbance and the sideroxylonal-A concentration of *E. melliodora* samples is depicted in Fig 4. The major correlation peaks for the first derivative transformation of the Log 1/R data occur at wavelength bands centred on 526, 561, 671, 1417, 1647 and 1800 nm. Other minor correlation peaks occur at wavelength bands centred on 615, 715, 787, 1711, 1985 and 2013 nm.

The highest correlations for the second derivative transformation of the Log 1/R data occur at 531, 622, 645, 685, 761, 1438 and 1800 nm.
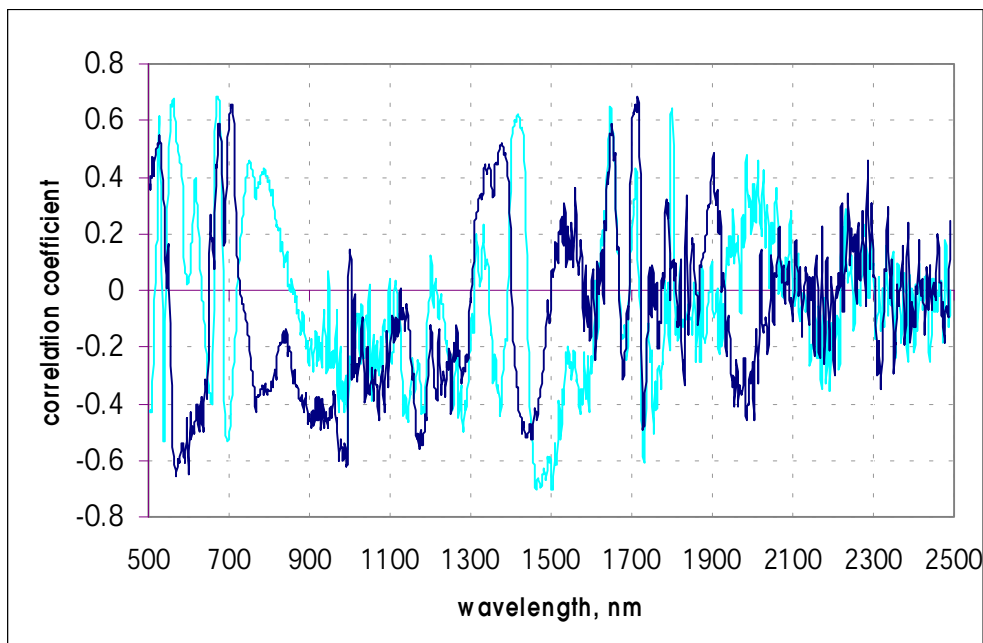

Fig. 4. Correlogram of sideroxylonal-A concentration for oven-dried ground leaf material (lighter line), compared with correlations for fresh leaf (darker line).

3.3   Whole fresh leaves

The validation data sets were predicted with coefficients of determination of 0.49 and 0.53 for the regression models using the first and second derivative transformations of the Log 1/R data sets, respectively (fig 5a,b).

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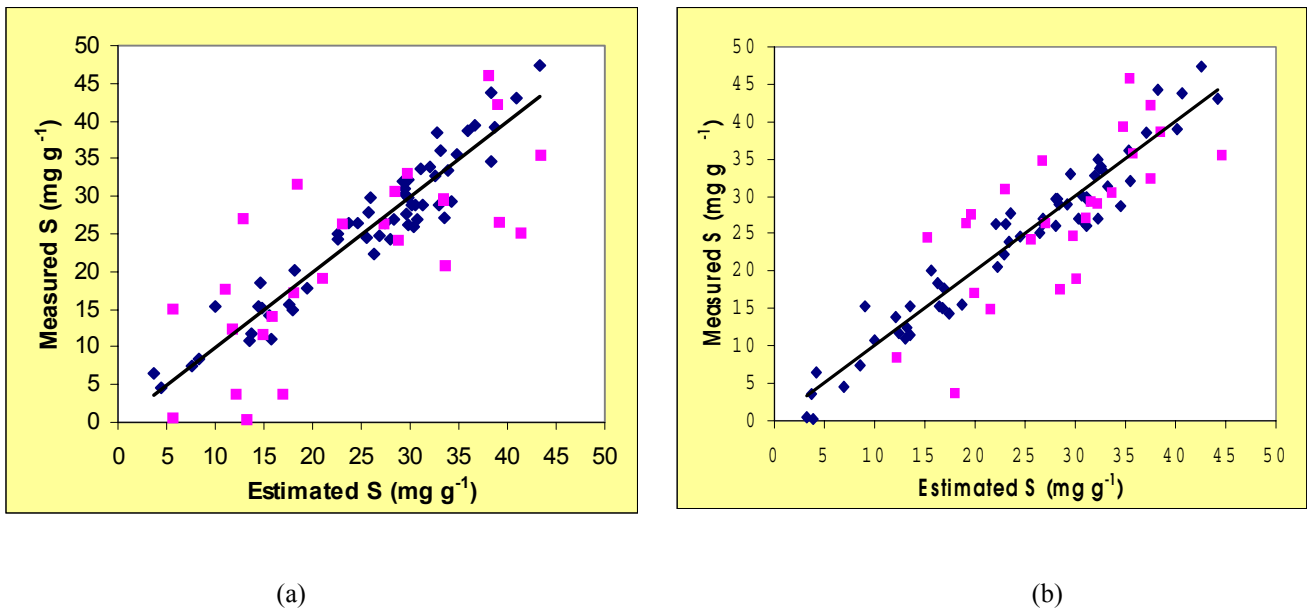<tr><td>(a)</td><td>(b)</td></tr>
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Fig 5. Plot of measured versus predicted sideroxylonal-A (S), using calibration regression equations generated for the whole, fresh leaf data set, for a) first derivative and b) second derivative Log 1/R data. The validation data is represented by lighter squares.

The 'best' calibration data set regressions for the first and second derivative data transformations were similarly ranked in terms of r^2 and SECV, although the SECV was lower for the former (see Table 1). The regression equations of the combined calibration and validation data sets show that the predictive value of the first derivative data transformation was superior to the second derivative data transformation through having a lower SECV (5.22 against 6.06) despite the higher r^2 (0.95 against 0.91) of the latter.

The major correlation peaks for the first derivative transformation of the Log 1/R data (plotted in figs 2 and 4) occur at wavelength bands centred on 528, 674, 707, 1378, 1651, 1716, 1904 and 2286 nm.

The highest correlations for the second derivative transformation of the Log 1/R data occur at 528, 556, 701, 1199, 1391, 1664 and 1713 nm.

4   DISCUSSION

Comparison of the results for the ground, dry and fresh leaf data sets reveals that both the first and second derivative transformations of the Log 1/R data are equally capable of predicting sideroxylonal-A concentrations. No single scatter correction consistently featured in the selected models. The optimal mathematical treatment for each of the three leaf treatment data sets occurred when the derivative was calculated over a gap of 8 nm.

Using first derivative transformations of the Log 1/R data, two spectral regions, centred on 674 nm and 1394 nm (although the latter varied between 1378 and 1417 nm) appeared highly correlated with sideroxylonal-A concentration across the three leaf treatments. The former coincides with the only spectral region picked out from each treatment using second derivative transformation data, namely at 682, 685 and 701 nm, for the ground, dry and fresh leaf data sets, respectively. Two wavelength regions (568/561 nm and 618/615 nm) exhibited high correlation in the ground and dry leaf data sets, but not in the fresh leaf data set. Three wavelength regions (526/528 nm, 1647/1651 nm and 1711/1716 nm) showed high correlation in the dry and fresh leaf data sets, but not in the ground leaf data set.

The second derivative transformations gave fewer matching regions of high correlation.. Apart from the 685 nm region, highlighted in all three datasets, the only other matching correlations were at 626/622 nm (ground and dry leaf data sets), 531/528 nm (dry and fresh leaf data sets), and 1404/1391 nm (ground and fresh leaf data sets).

The results from the fresh leaf measurements are of particular interest for assessing the capability to remotely estimate an important measure of habitat quality (concentrations of plant secondary chemicals) of eucalypt forests for folivorous marsupials. By comparing calibration equations and wavelength correlations obtained from reflectance measurements of whole, fresh leaves with those from dry/ground leaf material, it is possible to judge whether wavelengths identified from the MPLS calibration equations of the fresh leaf spectra are important, or perhaps merely artefacts of the data. Since the higher correlations in the fresh leaf first derivative transformation spectral regions centred on 674 and 1378 nm were identified in the other data sets, one may presume that these regions are significant. 1378 nm is close to an area of strong water absorption, and in the dry and ground leaf spectra the strongest correlations were actually centred at slightly longer wavelengths, around 1405 nm, where it is likely that the dominant absorption by water obscured that of sideroxylonal in the corresponding fresh leaf spectra. Other likely important spectral regions are those centred on 528 nm, 1651 nm, and 1716 nm, identified in both the fresh and dry whole-leaf data sets. Flinn et al. (1996) found that phenolics have a major absorbance around 1650 nm, and this wavelength has been used to separate forage samples containing high and low concentrations of phenolic constituents. The three correlation peaks identified in the freeze-dried, ground leaf spectra between 2300-2500 nm were not identified in either the fresh or dry leaf spectra. This may be due to the 'noisier' spectra obtained in this region when measured by the FieldSpec spectroradiometer. In future analyses we will investigate the predictive ability of regression models using only the wavelengths highlighted above, to further minimise the risk of overfitting.

A recent study has highlighted a role for terpenes in marsupial folivore–*Eucalyptus* interactions, whereby they appear to act as a cue to concentrations of toxic DFPCs in the leaves (i.e. a conditioned flavour aversion) (Lawler et al., 1999). Indeed, the same authors note that correlations between terpenes (e.g. cineole) and DFPCs have been found in several eucalypt species. It is possible, therefore, that wavelength correlations with sideroxylonal-A concentration may in fact relate to absorbance features of terpenes. As long as the correlation between the two substances is consistent this does not pose a problem and may even serve to enhance our predictions of DFPC's. To gain a better understanding of whether the wavelengths highlighted in this study are a direct consequence of absorption by sideroxylonal-A we plan to collect spectra of purified sideroxylonal-A, extracted as described in Lawler et al. (2000). Although Wessman et al. (1988) pointed out that the exact wavelengths of pure compound absorption will not necessarily appear in near infrared spectroscopy equations, due to the presence of other compounds in the mixture tending to broaden and confound their effect, if the regression equations include terms that appear close to the constituent's absorbing wavelengths we can have greater confidence in the robustness of the equations, particularly for the estimation of sideroxylonal-A concentration at sites distant from the training sites.

With the continuing clear-cutting of Australia's forests it is imperative to accurately assess the quality of forest blocks as habitat for arboreal marsupials. Management of forests for wildlife will require accurate maps of the diversity and extent of habitats over large areas and often difficult terrain. Even with NIRS it will be impractical to assess all but the smallest forest blocks, or subsections of larger blocks. High spectral resolution airborne imaging spectrometry offers scope for a faster, large scale assessment of habitat quality. This is the first stage in part of a wider study aimed at tracking minor absorption features in reflectance measurements from the laboratory to the field, to assess whether we can measure the palatability of eucalypt canopies. If successful, this will provide the first opportunity to extend laboratory-based data to a scale sufficient to answer fundamental questions at the landscape level pertinent to the management and conservation of arboreal folivores.

5   CONCLUSION

In this study we have demonstrated that imaging spectroscopy can be used to measure the concentration of a eucalypt PSM (sideroxylonal-A, known to play an important role in deterring feeding by marsupial folivores), in the laboratory using intact, fresh leaf samples, with reasonable predictive value. This is despite the dominant effect of absorption by water in fresh leaves, which obscures some but not all of the useful absorption features. A number of wavelength regions highly correlated with sideroxylonal-A concentration in the fresh leaf spectra were also found to be highly correlated in the dry and/or ground leaf spectra, suggesting these are likely to have some physical significance rather than being attributable to noise. In particular the first derivative transformation spectral regions centred on 674 and 1378 nm are likely to be useful for predictive purposes since these were identified in all three data sets. These results indicate that the remote estimation of habitat quality of eucalypt forests for folivorous marsupials is feasible, dependent on the successful extraction of the foliar spectra from airborne/spaceborne imaging spectrometry data.

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