

Spectral sensing of foliar water conditions in two co-occurring conifer species: *Pinus edulis* and *Juniperus monosperma*

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Abstract

Many fundamental ecosystem properties and dynamics are determined by plant water stress, particularly in dryland ecosystems where water is usually limiting. Indeed, under severe drought, plant water stress and associated insect infestations can produce landscape-scale mortality. Despite the fundamental importance of plant water stress in determining properties and dynamics at ecosystem and landscape scales, approaches for remotely sensing plant water stress are largely lacking, particularly for conifers. We evaluated the remotely sensed detection of foliar drought stress in two conifer species, *Pinus edulis* and *Juniperus monosperma*, which are co-dominants of extensive-juniper woodlands in North America, the first of which experienced extensive mortality in association with a recent drought. Needle spectra were made on these species in the field using an integrating sphere and portable spectrometer. Two indices of foliar water condition, plant water content (% of dry mass) and plant water potential, were compared to five spectral analyses: continuum removal of the 970 and 1200 nm water absorption features, the Normalized Difference Water Index (NDWI), the Normalized Difference Vegetation Index (NDVI), and the red edge wavelength position. For *P. edulis*, plant water content was significantly correlated with four of the five indices: NDVI ($R^2=0.71$) and NDWI ($R^2=0.68$) which exhibited stronger relationships than 970 nm continuum removal ($R^2=0.57$) or red edge position ($R^2=0.45$). All five indices were significantly correlated with *P. edulis* water content when trees undergoing mortality were included in analyses ($R^2=0.60-0.93$). Although the correlations were weaker than for plant water content, plant water potential was significantly correlated with NDWI ($R^2=0.49$), 970 nm ($R^2=0.44$), NDVI ($R^2=0.35$), and red edge ($R^2=0.34$); again all five indices had significant relationships when trees undergoing mortality were included ($R^2=0.51-0.86$). The relationships were weaker for *J. monosperma*: water content was significantly related to 970 nm ($R^2=0.50$) and 1200 nm ($R^2=0.37$) continuums and NDVI ($R^2=0.33$), while water potential was related only to 1200 nm ($R^2=0.40$). Our results demonstrate a critical link between plant physiological characteristics tied to water stress and associated spectral signatures for two extensive co-occurring conifer species.

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1. Introduction

Plant water relations determine many fundamental ecosystem patterns, processes, and dynamics (Lambers et al., 1998; Waring & Running, 1998). In particular, foliar

water content and associated water potential is a primary limiting factor for plant transpiration and carbon gain. The constraint imposed by water on these processes is particularly great in dryland ecosystems where water is usually limiting (Ludwig et al., 1997; Noy-Meir, 1973). Foliar water content is temporally and spatially variable in response to high heterogeneity in the distribution of precipitation and associated soil moisture (Breshears et al., 1997b; Loik et al., 2004; Padien & Lajtha, 1992). Variation in foliar water condition is of particular importance during drought, when plant water stress can

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cause cavitation, in which embolisms break the water column (Pockman & Sperry, 2000), that can lead to mortality of individual plants, sometimes at landscape scales (Allen & Breshears, 1998).

Ecologists have used field measurements of leaf water content and leaf water potential for several decades as sensitive indicators of water status. Leaf water content and water potential are related to several water status variables and both measures have been reported extensively in the literature. Despite the potential value of these measurements, the requirements for pre-dawn water potential measurements to estimate soil moisture status and minimum plant water stress levels and diurnal measurements to estimate maximum water stress impose severe limits on the number of samples that can be measured. The relationship between water content and water potential has long been used by physiologists to quantify water status by plotting moisture release curves, in which the relative water content (the leaf water weight/leaf turgid weight) is graphed against the reciprocal of water potential, to estimate the water content at zero turgor, the osmotic and matrix potentials, among others. The need to hydrate samples and measure fresh and dry weights to obtain relative water content imposes significant limitations for using this technique over large areas or over extended periods. Both Cohen (1991b) and Hunt (1991) have expressed reservations about the usefulness of a relative water content index for remote sensing applications.

Foliar water status of conifer species is of particular interest to ecologists due to their extensive distribution and frequent dominance in dryland landscapes, where variation in water status is especially important. Nonetheless, it is impractical to obtain the numerous near-simultaneous estimates of plant water status that are needed to assess landscape-scale function and dynamics. The measurement problem becomes impossible when such data are needed to monitor a region over an extended period of time. Consequently, landscape-scale assessments of plant water status are only practically pursued through modeling (Waring & Running, 1998).

Remote sensing offers the potential to estimate foliar water condition, even on a routine basis. Variance in water content of leaves is a primary physical driver for variance in reflectance properties in the infrared region (Gao, 1996; Gao & Goetz, 1994, 1995; Jacquemoud & Ustin, 2003; Ustin & Curtiss, 1990; Ustin & Jacquemoud, 2003; Ustin et al., 1998, 2004). However, assessment of conifer water condition has traditionally been difficult to measure and quantify even in laboratory measurements due to branch and leaf geometry (Brand, 1987) and optical properties (Ustin et al., 2004). Although the potential for assessment of water condition via evaluation of spectral properties of foliage has been demonstrated, previous studies have focused primarily on leaves of broadleaf species grown for this purpose (Adams et al., 1999; Bowman, 1989; Ceccato et al., 2001; Inoue et al., 1993; Penuelas et al.,

1993; Peñuelas & Inoue, 1999; Yu et al., 2000) or collected in the field (Blackburn, 1999; Gao, 1996; Gao & Goetz, 1994; Gitelson et al., 1996; Hunt et al., 1987).

Most studies that have investigated detailed spectral properties of conifer needles (Danson et al., 1992; Daughtry et al., 1989; Mesarch et al., 1999; Ustin & Curtiss, 1990) have not focused on water content. However, Cohen (1991a,b) examined relationships between Landsat band indices and relative water content in laboratory experiments on needles of Coulter pine and lodgepole pine, and showed that ratios of red to near infrared (NIR) and NIR to short-wave-infrared (SWIR) were correlated with water content and water potential.

Numerous correlations between spectral bands or band ratios related to water status have been developed (e.g., Datt, 1999; Inoue et al., 1993; Ripple, 1986; Yu et al., 2000). Some spectral indices to assess water content have used Landsat Thematic Mapper (TM) satellite bands, including a pigment index, NDVI (Penuelas et al., 1993); water absorption index, WI (R_{895}/R_{972} ; Penuelas et al., 1993); Moisture Stress Index (R_{1599}/R_{819} ; Hunt & Rock, 1989); and Normalized Difference Infrared index, NDII ($[R_{819}-R_{1649}]/[R_{819}+R_{1649}]$; Hardisky et al., 1983).

Some landscape-level studies to detect water condition have involved conifers to a greater (Gao & Goetz, 1994, 1995) or lesser extent (Gao, 1996; Serrano et al., 2000; Ustin et al., 1998; Zarco-Tejada et al., 2003). An early hyperspectral study by Riggs and Running (1991) had limited success measuring induced water stress on conifer canopies using the AIS airborne instrument and analysis techniques available at the time. To date, few studies have tested the ability of spectral measurements to detect water condition of conifers at the needle level. Although establishment of needle-level relationships alone is insufficient to detect patterns at larger ecosystem and landscape scales in imagery, it is a necessary component for developing such methods.

Narrow-band spectroscopy measurements like the Equivalent Water Thickness (EWT) that integrate reflectance from R_{867} through R_{1049} (Green et al., 1993) or the water thickness integrating from R_{867} through R_{1068} (Roberts et al., 1998) are obtained by modeling atmospheric water vapor and liquid water in imaging spectrometry data. Serrano et al. (2000) showed in AVIRIS data that pigments, water, and EWT are strongly correlated and show similar relationships to relative water content (RWC), with NDWI providing the best correlation. The continuum removal indices at 970 and 1200 nm integrate responses over water absorption features producing relationships similar to the EWT and WT measures derived from atmospheric calibration of AVIRIS data.

The red edge, a narrow band index that estimates foliar pigment concentration, provides an alternative to the more commonly studied Normalized Difference Vegetation Index (NDVI), which is correlated with water through relationships with leaf area and chlorophyll in foliage. The red edge

is less subject to background effects than NDVI, which, although not an issue for this leaf-level study, is an important consideration in applying these methods to hyperspectral images of piñon–juniper woodlands due to the low canopy cover fraction in these woodlands.

For this study, needle spectra of these species were collected in the field using an integrating sphere and portable spectrometer. Our overall objective was to evaluate the relationships between foliar water content and spectral signals in two coniferous species: *Pinus edulis* Englem. (Colorado piñon pine) and *Juniperus monosperma* [Englem.] Sarg. (one-seed juniper), co-dominants of the extensive piñon–juniper woodlands of North America (West, 1988). Sampling at a semiarid woodland site of ongoing ecological interest in northern New Mexico, USA, we used field-based measurements at the needle level to evaluate the ability of a suite of spectral analyses—including continuum removal of the 970 and 1200 nm water absorption features, the Normalized Difference Water Index (NDWI), the Normalized Difference Vegetation Index (NDVI), and the red edge wavelength position—to assess two ecological fundamental indicators of plant water stress: foliar water content and plant water potential.

2. Methods

2.1. Study site

The study was conducted at the Mesita del Buey piñon–juniper woodland research site in northern New Mexico, USA, within Technical Area 51 of the Los Alamos Environmental Research Park (latitude 35.85° N, longitude 106.27° W, elevation 2140 m). The site has been the subject of studies of microclimate (Breshears et al., 1997b, 1998; Martens et al., 2000; Wilcox et al., 2003a,b), plant physiology (Breshears et al., 1997a; Lajtha & Barnes, 1991; Lajtha & Getz, 1993), and plant community interactions (Martens et al., 1997, 2001; Padien & Lajtha, 1992). The area has a temperate montane climate, with annual precipitation of approximately 400 mm, mainly in the form of winter snowfall and late-summer precipitation (Bowen, 1990). The soils are Hackroy clay loam, derived from volcanic tuff (Nyhan et al., 1978); soil depth at the Mesita del Buey site varies from 0.33 to 1.25 m (Davenport et al., 1996). Allen (1989) describes the landscape ecology of this area, including historical land use and disturbances such as fire, drought, and insect infestations. The dominant overstory species are *P. edulis* and *J. monosperma*. Overstory canopy coverage is approximately 50% (Martens et al., 1997, 2000; Padien & Lajtha, 1992). Ground cover in intercanopy areas adjacent to the study site is about 85% with approximately 50% from cryptogamic crust, 13% from grass (primarily *Bouteloua gracilis* (H.B.K.) Lag.), 2% semi-shrub, 1% forb, and 18% litter (Wilcox, 1994); canopy

areas are covered with litter and contain few herbaceous plants.

To obtain measurements over the widest range of foliar water conditions, we sampled two additional areas adjacent to Mesita del Buey. The first was a nearby piñon–juniper woodland located next to a paved parking lot and buildings that allowed it to receive additional runoff following precipitation events, thereby likely reducing water stress relative to Mesita del Buey. The second was an experimental plot, 50 m × 50 m in size, within the Mesita del Buey piñon–juniper woodland, in which rainfall was excluded to enhance the effects of drought. Added drought stress was created by covering the ground with a sheet of plastic which was tightly fitted to the base of each tree, preventing infiltration of precipitation. Our samples included some *P. edulis* trees that had pale foliage and appeared to have undergone mortality, which was confirmed by visual observations of needle senescence and leaf fall from those trees in subsequent weeks. Our analyses for *P. edulis* were conducted both excluding and including these samples to assess metrics related to water stress during non-mortality stress conditions and during mortality.

2.2. Sampling design

For both species, we selected a set of trees from the three site locations that provided the largest range of water stress for this region, which was independently supported by visual estimates of needle color and overall tree health. Nineteen samples were collected from *P. edulis* trees (two trees from the parking lot area, five from the drought-induction plot, 12 trees from the surrounding Mesita del Buey woodland), which included four trees with pale foliage that were later confirmed to be senescent, as noted above. Additionally, nine *J. monosperma* trees were sampled, all of which were located in the drought-induction plot (fewer *J. monosperma* trees were needed as none showed signs of mortality).

Within each tree, we collected needles in a consistent manner for statistical analysis. A first set of needles, intact on twigs, were obtained to measure predawn plant water potential and a second set was obtained for percent water content and spectral analysis. Needles were collected within each tree: three predawn water potential twigs from each tree were collected at a height of 1–2 m, from different branches of *P. edulis* and from different stems of *J. monosperma*. For the second set of needles from each tree, three needle-bearing fascicles were collected from the north side of each tree at a height of 1–2 m. For *P. edulis*, we used only the youngest age-class needle whorl with needles large enough (>2 cm in length) to fit over the port of the LI-COR 1800 integrating sphere (LI-COR, Lincoln, NB). Preliminary testing of water content variation on branches within trees indicated that the measurements were representative of the whole tree, with no significant variability due to cardinal direction or height of needles on the tree (data not shown).

These results are consistent with the open crown structure of these species and the high radiation environment at the site. Additionally, they are consistent with previously reported measurements on these species at this site (Breshears et al., 1997a), which showed that within-plant water potential generally does not vary more than 0.2 MPa. Consequently, both sets of needles were considered to represent a common expression of water relation properties and data from both were utilized in the analyses. All trees were sampled on either 21 or 22 August 2002 for predawn plant water potential, foliar water content, and spectral measurements, with all measurements for a given tree obtained on the same day. The range of variability in plant water potential was at the extreme observed over the prior 10 year period (D. D. Breshears, personal observation; Breshears et al., 1997b), providing a valuable opportunity to evaluate spectral detection of naturally induced water stress over a wide range of leaf water conditions.

2.3. Foliar status measurements

Plant water potential was measured before dawn for each of the trees as described in Breshears et al. (1997a). Twigs were placed in plastic bags and kept cool and in the dark until measurement, usually within 1 h (previous studies indicate little expected change in plant water potential for samples handled this way within this time interval; Breshears et al., 1997a). Predawn plant water potential was measured to the nearest 0.05 MPa (PMS Model 1000 pressure chamber, Corvallis, OR) on two twigs (the third was reserved as a replacement in case of damage). Relative to the range of water potential among trees (range=2.0 MPa for *P. edulis* and 4.3 MPa for *J. monosperma*), within-tree variation was small (S.D.=0.11 MPa for *P. edulis* and 0.10 MPa for *J. monosperma*). Four *P. edulis* samples had lower water potentials than the -6.5 MPa limit of the chamber and consequently those samples were excluded from the initial statistical analyses but were used in subsequent analyses that included trees undergoing mortality. In the later case, we assumed the water potential of these trees was equal to -6.5 MPa, which introduced a systematic bias that under-represents the most water stressed samples.

The second set of needles was collected during daylight hours following the same procedures and measured within 2 h. The needles were removed from the twigs and divided; one subset was used for water content analysis, the other for spectral measurement. To aid construction of spectral samples (see below), the larger and straighter needles of *P. edulis* were generally selected for spectral sampling. Because of the small within-tree variability, this measurement requirement for the LICOR integrating sphere was not considered to have biased the results. To estimate water content as a % of dry mass, the needles were weighed fresh, dried for approximately 24 h at 60 °C, and then re-weighed for dry mass. A subset of samples was dried for intervals

longer than 24 h and reweighed to ensure that 24 h was sufficient to dry needles to constant dry weight.

2.4. Spectral measurements and analysis

The set of needles used for spectral measurements was measured inside a LI-COR LI 1800 Portable Integrating Sphere that had an ASD Field Spec Pro Full Range spectrometer (Analytical Spectral Devices Inc., Boulder, CO) with a fiber-optic fitted into the light-tight port. LI-COR modified the light source of the integrating sphere by removing the heat filter to permit spectral measurements at longer wavelengths.

Because conifer needles are too small to fill the sample port field-of-view, they were arranged side-by-side to form solid mats, following the technique described by Daughtry et al. (1989). The measurements are sensitive to the spacing and pre-treatment of the needles. Daughtry et al. (1989) has suggested an improvement to the basic method by painting the back (adaxial side) of the needles with opaque black paint and spacing them at a fixed distance to produce a more exact characterization of the reflectance, absorbance, and transmittance of the samples. Recently, Mesarch et al. (1999) tested this method by analyzing images of needle samples and measuring the effect of gaps on the measured transmittance and found that fixed spacing of needles could also introduce errors in transmittance measurements. Mesarch et al. (1999) established a rough threshold of a 0.2 gap fraction for unpainted needles, below which “non-gap” transmittance measurements are valid. Because our ultimate goal is to assess the viability of landscape-level reflectance measurements, which is less gap sensitive (Daughtry et al., 1989), we measured only needle reflectance using unpainted needles packed together with closest possible spacing. We used image analysis to record the actual gap fractions.

The needles were arranged, side-by-side, flat side down, across a 20 mm opening in a vinyl mount for *P. edulis* and for *J. monosperma*, in as contiguous a manner possible without overlapping needles or leafy shoots. The mount was centered over the integrating sphere port to fill the opening with leaves. Double-sided clear tape on the vinyl mount aligned the initial placement of the needles, which were then secured in place with a second layer of single-sided tape. Care was taken to minimize the gap between needles, although some space was unavoidable, particularly for the irregularly shaped *J. monosperma* shoots. The needles were placed at the port of the integrating sphere with the rounded side facing the light source, and measured for 10 repetitions of 10 iterations at 100 ms each (10 s total integration time per sample). Each measurement was completed within 2 min after optimizing the instrument for the intensity of the integrating sphere light source and making a reference reflectance measurement using a Spectralon 99% reflectance standard (Labsphere Inc., North Sutton, NH). At the beginning of each day, reflectance spectra of erbium oxide and 10% reflectance Spectralon were recorded to ensure the

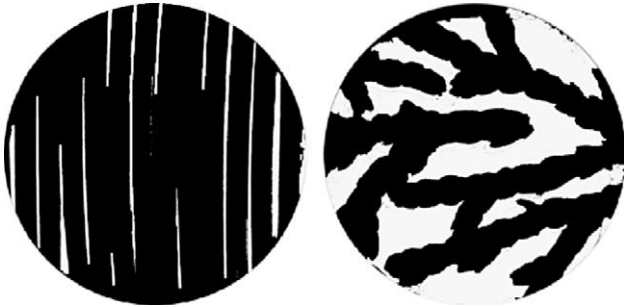


Fig. 1. Magnified example of the field of view of the spectrometer for a sample of *P. edulis* (left) and *J. monosperma* (right). Gap (white) and foliage (black) areas have been filled to aid measurement of their relative proportion, i.e., the “gap fraction” of the sample. Gap fraction is 0.06 for the *P. edulis* sample, 0.38 for the *Juniper*.

consistency of the wavelength and reflectance calibrations of the spectrometer.

After the reflectance was recorded for each sample, it was placed on a light table and a digital picture was recorded using a Canon G2 4.0 megapixel digital camera. The camera was set at the highest resolution in macro mode and placed with the lens 0.24 m from the sample. The digital pictures were analyzed to quantify the gap fraction for packets of needles. Polygons of gap and non-gap were manually selected in Adobe Photoshop 6.0 (Adobe Systems, Inc. San Jose, CA), and a binary image was created as shown in Fig. 1. The resulting images were exported to SigmaScan Pro 5 (SPSS Inc., Chicago, IL), and a pixel intensity threshold was applied to the image to compute the gap fraction for each sample.

Reflectance data were analyzed using the Spectral Analysis and Management System (Rueda, 2002) to extract five indices for each of the samples: the Absorption Index at 970 and 1200 nm wavelengths, the Normalized Difference Water Index (Gao, 1996), the Normalized Difference Vegetation Index (NDVI), and the red edge position (Horler et al., 1983). Before analysis, spectral data were smoothed using a Savitzky and Golay (1964) filter to mitigate the effects of sensor noise. The Absorption Index (AI) is a modification of the continuum removal technique (Clark & Roush, 1984) and was calculated from the ratio of the area under the water absorption continuum (a) between the two local maxima (“shoulders”) and the area connecting the shoulders (s). The trapezoidal method of integration was used to determine these areas, where

$$AI = 1 - (a/s).$$

We calculated the AI of the absorption features centered at 970 nm and 1200 nm.

The Normalized Difference Water Index (NDWI) ratios the normalized reflectance (ρ =reflectance) at 860 and 1240 nm, as:

$$NDWI = (\rho(860 \text{ nm}) - \rho(1240 \text{ nm})) / (\rho(860 \text{ nm}) + \rho(1240 \text{ nm})).$$

The NDVI is calculated, as ρ at the given wavelength, as:

$$NDVI = (\rho(860 \text{ nm}) - \rho(690 \text{ nm})) / (\rho(860 \text{ nm}) + \rho(690 \text{ nm})).$$

Red edge position is an index of chlorophyll absorption, measured as the wavelength at the inflection point of the derivative reflectance at the long wavelength edge of the chlorophyll absorption feature, located between 680 and 725 nm. In stressed plants, this edge shifts to shorter wavelengths as the width and depth of the chlorophyll absorption feature narrows and decreases due to chlorosis. We calculated the red edge position by determining the wavelength position of the maximum rate of change of the linear approximation of the differential along the red edge interval.

For both *P. edulis* and *J. monosperma*, linear regressions were conducted to assess the relationship for water content or water potential and each of the five spectral analyses: 980 nm AI, 1200 nm AI, NDVI, NDWI, and red edge position.

3. Results

The gap fraction measured for *P. edulis* samples averaged 0.06 with a standard deviation of 0.04, while gaps for *J. monosperma* averaged 0.37 with a standard deviation of 0.07. Thus, the *P. edulis* samples met the criteria of 0.2 gap fraction proposed by Mesarch et al. (1999) but *J. monosperma* samples exceeded this threshold. Representative spectra from high and low water content samples for both species are shown in Fig. 2. Low water content in the “dry” *P. edulis* is evident by the high reflectance and presence of cellulose and other dry

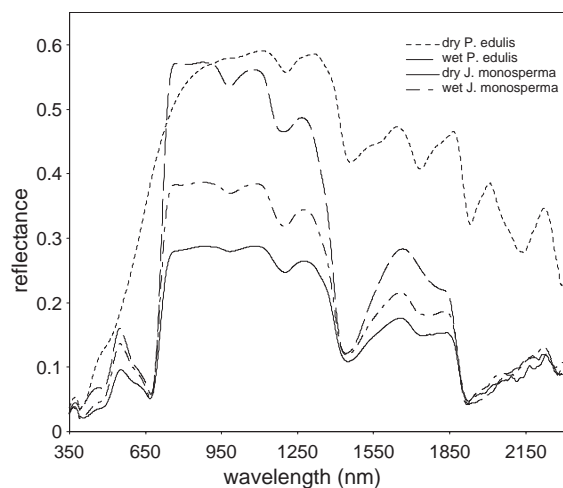


Fig. 2. Examples of high and low water content spectra of both *P. edulis* and *Juniper*. Note that the *J. monosperma*'s albedos are lower due to the larger gap fraction between the needles, resulting in less of the available light being reflected to the sensor.

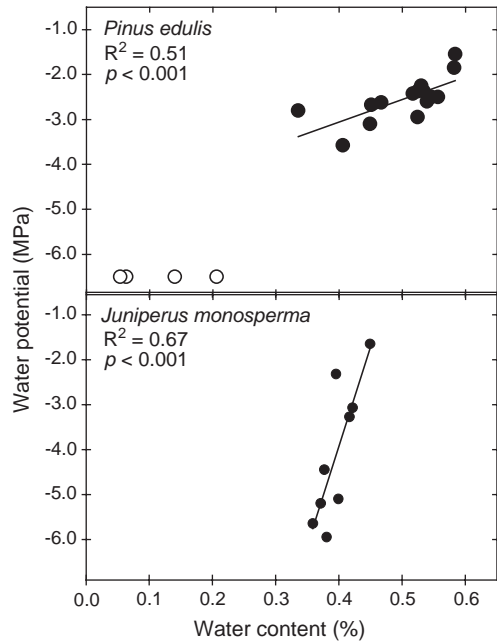


Fig. 3. Water content (% mass) and water potential (MPa) for foliage samples used in the study for *P. edulis* and *J. monosperma*. Open symbols for *P. edulis* are for trees that were undergoing mortality during the measurements.

plant absorption features in the shortwave-infrared. In contrast, the high and low water content *J. monosperma* shoots do not show strong spectral differences, consistent with the lower desiccation experienced by this species. For both species, however, water potential was correlated with water content, as expected (Fig. 3).

Water content of *P. edulis* was correlated with four of the five spectral measurements when trees undergoing mortality were excluded (Fig. 4; predictive relationships provided in Table 1). Despite the small sample size, many of these relationships were statistically significant at $p < 0.05$ or better. These results meet expected trends because spectral absorption near 980 and 1240 nm in the near-infrared is based on the physical property of water. However, the sensitivity of the spectral measurement to changes in water content and water potential over the limited biological ranges experienced under field conditions has been a concern in past studies. The relationship with water content for *P. edulis* was stronger with NDVI ($R^2=0.71$) and NDWI ($R^2=0.68$) than with the 970 nm AI ($R^2=0.57$) or the red edge position ($R^2=0.45$). When foliage samples from *P. edulis* that were undergoing mortality were included, all five spectral measurements were significantly correlated with water content ($R^2=0.60$ – 0.93 ; Table 1).

Although the remote sensing measurements do not directly measure water potential, they are indirectly correlated through the relationships with water content and chlorophyll content. The water potential of the *P. edulis* trees from which samples were taken, excluding trees undergoing mortality, was also correlated with the

same four of the five spectral measurements, although these relationships were weaker than those for water content (Fig. 5). The strength of the relationship was somewhat better for NDWI ($R^2=0.49$) and the 970 nm AI

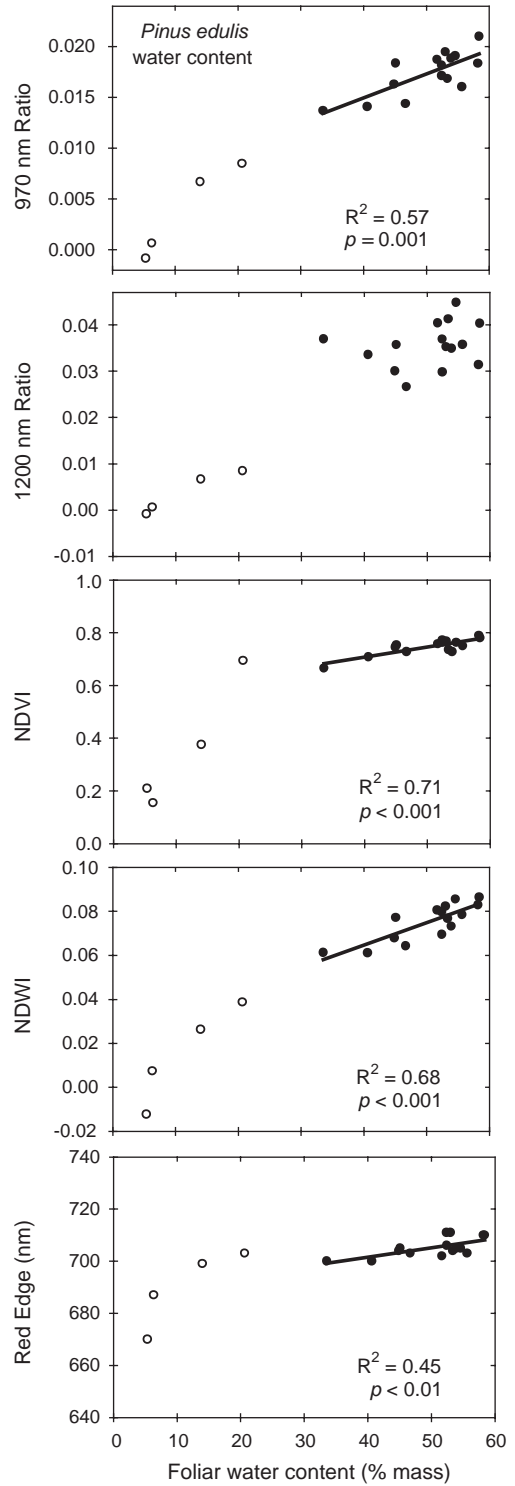


Fig. 4. Regression of *P. edulis* water content for five spectral indices. Reported relationships exclude trees undergoing mortality (open symbols); predictive relationships reported in Table 1. NDVI=Normalized Difference Vegetation Index; NDWI=Normalized Difference Water Index.

Table 1

Linear regression results between two metrics of plant water status and five spectral indices for two species (N.S.=not significant at $p \leq 0.10$)

Species	Water metric	Index	Excluding trees undergoing mortality					Including trees undergoing mortality					
			R^2	p	Slope	Intercept	N	R^2	p	Slope	Intercept	N	
<i>Pinus edulis</i>	Water content	970 nm	0.57	0.001	0.023	0.006	15	0.93	<0.001	0.035	0.000	19	
		1200 nm	0.06	0.37	N.S.	N.S.	15	0.60	<0.001	0.030	0.020	19	
		NDVI	0.71	<0.001	0.383	0.555	15	0.82	<0.001	0.992	0.247	19	
		NDWI	0.68	<0.001	0.102	0.024	15	0.93	<0.001	0.153	-0.002	19	
		red edge	0.45	0.01	36.049	687.141	15	0.65	<0.001	43.513	683.669	19	
	Water potential	970 nm	0.44	0.01	0.003	0.025	15	0.86	<0.001	0.003	0.026	19	
		1200 nm	0.06	0.40	N.S.	N.S.	15	0.60	<0.001	0.003	0.043	19	
		NDVI	0.35	0.02	0.038	0.845	15	0.70	<0.001	0.984	0.094	19	
		NDWI	0.49	0.01	0.012	0.107	15	0.85	<0.001	0.015	0.113	19	
		red edge	0.34	0.02	4.439	716.556	15	0.51	<0.001	3.954	715.349	19	
	<i>Juniperus monosperma</i>	Water content	970 nm	0.50	0.03	0.033	0.002	9	Not applicable				
			1200 nm	0.37	0.08	0.153	-0.017	9					
			NDVI	0.33	0.10	0.714	0.411	9					
			NDWI	0.03	0.67	N.S.	N.S.	9					
			red edge	0.11	0.38	N.S.	N.S.	9					
Water potential		970 nm	0.09	0.43	N.S.	N.S.	9						
		1200 nm	0.40	0.07	0.056	0.003	9						
		NDVI	0.02	0.68	N.S.	N.S.	9						
		NDWI	0.03	0.66	N.S.	N.S.	9						
		red edge	0.03	0.63	N.S.	N.S.	9						

($R^2=0.44$) than for NDVI ($R^2=0.35$) or the red edge position ($R^2=0.34$). When the trees undergoing mortality were included, water potential was significantly correlated with all five spectral measurements and relationships were stronger ($R^2=0.60$ – 0.86 ; Table 1), presumably because of the greater range of values.

Relationships between spectral measures and both water content and water potential of *J. monosperma* were weaker than those detected for *P. edulis*, as expected from the larger gap fraction. Nonetheless, for *J. monosperma* at least three spectral indices were significantly related to water content and one to water potential. *J. monosperma* water content (Fig. 6) was significantly related to the 970 nm AI ($R^2=0.50$), and to a lesser extent the 1200 nm AI ($R^2=0.37$) and NDVI ($R^2=0.33$; predictive relationships provided in Table 1). Surprisingly, neither red edge position nor NDWI was related to water content. Water potential of *J. monosperma* (Fig. 7) was related only to the 1200 nm AI ($R^2=0.40$; predictive relationships reported in Table 1).

In summary, the spectral measurements generally were more tightly correlated with water content than water potential and the relationships were generally stronger between the spectral analyses and the physiological states of *P. edulis* than that of *J. monosperma*. Although the NDWI showed a good relationship with water content and water potential of *P. edulis*, it was not related to the water status of *J. monosperma*. The most robust indicators of water condition, both of which had significant relationships for *P. edulis* water content and water potential, were the 970 nm AI, which had a significant relationship with *J. monosperma* water content, and NDVI, which had a significant relationship with water potential.

4. Discussion

4.1. Leaf optical properties

The optical properties of leaves control the reflectance spectra of plant leaves and although broadly understood, many specifics remain to be elucidated (Jacquemoud & Ustin, 2003; Ustin & Jacquemoud, 2003). The primary absorptions of water are greatest in spectral bands centered at 1450, 1940, and 2500 nm, with important secondary absorptions at 980 nm and 1240 nm (Carter, 1991). Reflectance in dry leaves is influenced by dry carbon compounds like cellulose and lignin, among other plant compounds that comprise the mass of dry conifer needles. The action spectrum of chlorophyll and photosynthetic pigments affects absorbance of energy at wavelengths shorter than 700 nm, water affects absorbance at wavelengths longer than 950 nm while leaf dry matter has minimal ($\sim < 0.1$) absorbance in the visible and near-infrared, and absorbs more strongly only at wavelengths longer than 1250 nm. Therefore, water is the primary molecule absorbing energy in the wavelength regions used for AI and NDWI, although leaf anatomy and biochemistry clearly affect the measurements.

In this study we investigated empirical methods for rapid assessment of foliar water stress and water content and demonstrated that a number of narrow band indices can be used to assay water status in conifer needles. The correlation of water potential to the indices we studied was amplified by the high level of drought stress leading to *P. edulis* undergoing mortality during the measurements. The water potentials measured were

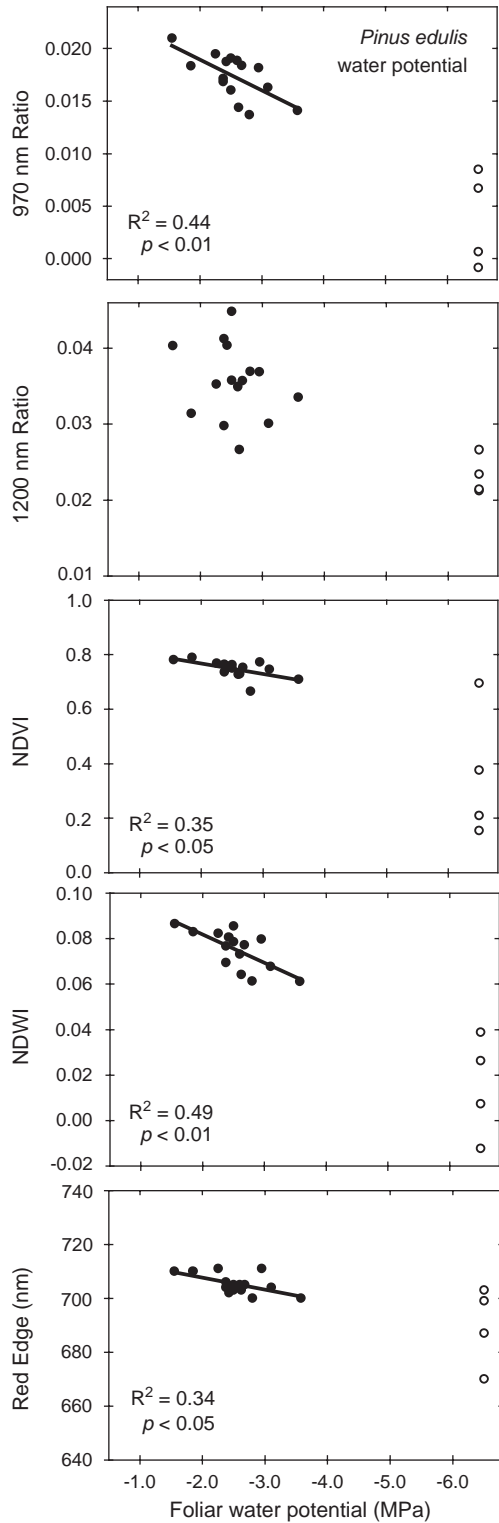


Fig. 5. Regression of *P. edulis* water potential for five spectral indices. Reported relationships exclude trees undergoing mortality (open symbols); predictive relationships reported in Table 1. NDVI=Normalized Difference Vegetation Index; NDWI=Normalized Difference Water Index.

at or near zero turgor and thus, near the linear portion of the relationship between water content and water potential.

4.2. Measurement issues

Greater correlation was achieved in relating spectral measurements to the foliar water status of needles of *P.*

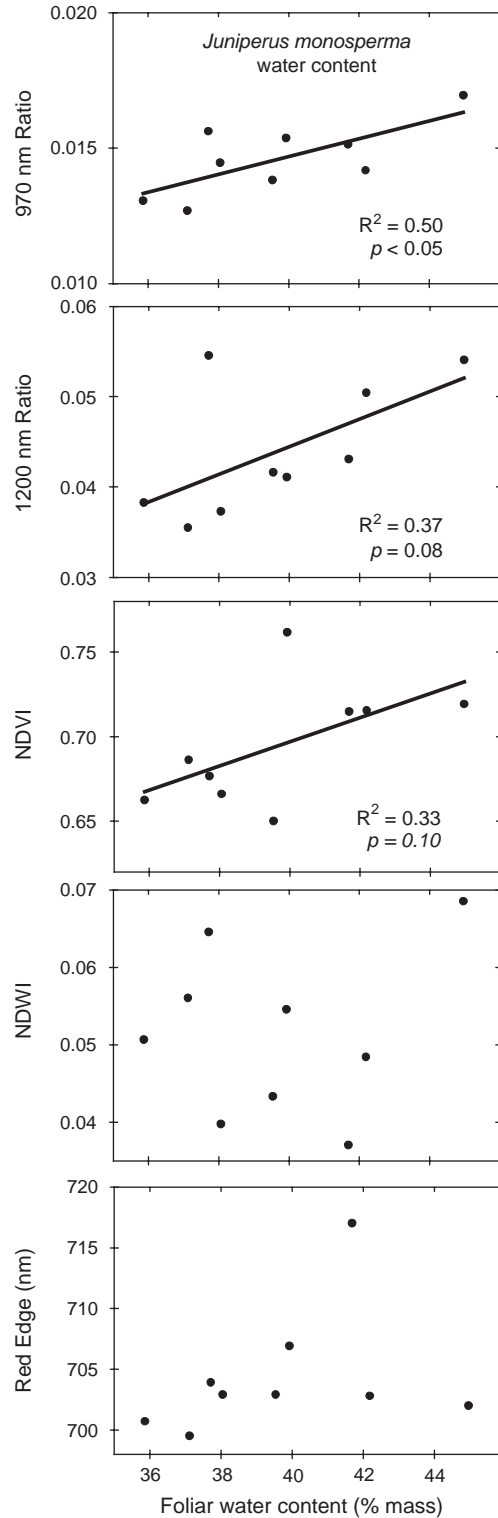


Fig. 6. Regression of *J. monosperma* water content for five spectral indices; predictive relationships reported in Table 1. NDVI=Normalized Difference Vegetation Index; NDWI=Normalized Difference Water Index.

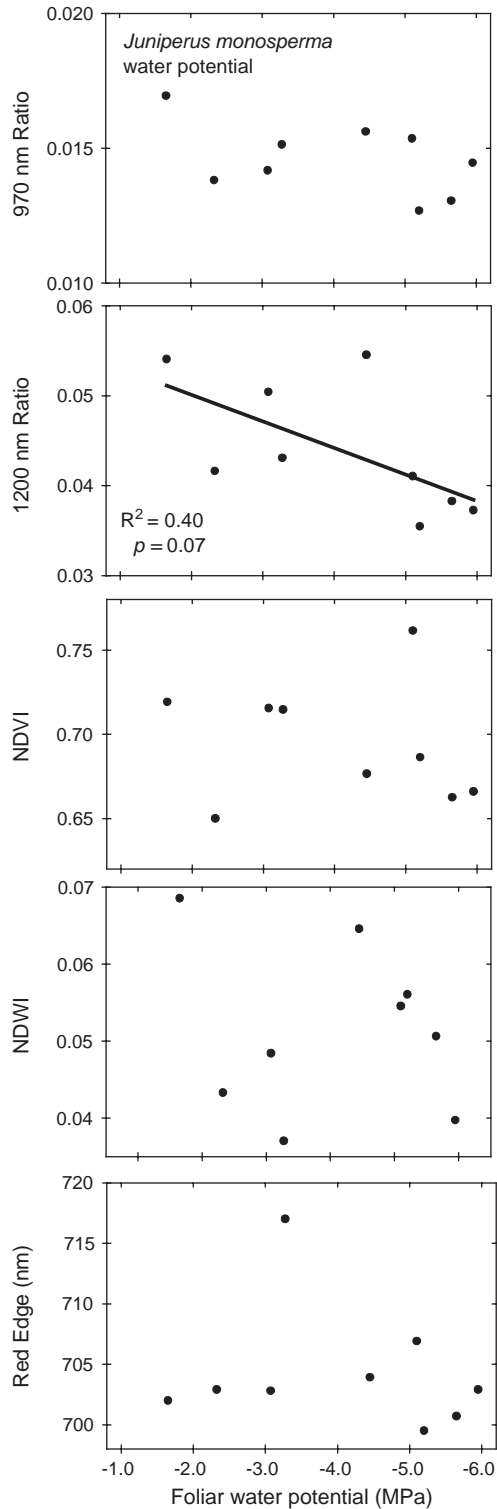


Fig. 7. Regression of *J. monosperma* water potential for five spectral indices; predictive relationships reported in Table 1. NDVI=Normalized Difference Vegetation Index; NDWI=Normalized Difference Water Index.

edulis than to those of *J. monosperma*. This is partially attributable to the six times larger average gap fraction in *J. monosperma*. This difference was due to the denticulate growth form of its leafy shoots, which prevented placing

them as tightly as the straighter piñon needles. The greater gap fraction in *J. monosperma* resulted in lower overall reflectance and albedo. All five of the spectral analyses used in this study are resistant to errors introduced by differences in total albedo: the absorption indices, NDWI and NDVI ratio use spectral intensities rather than absolute values, and the red edge position measures only wavelength. Nonetheless, the reduced albedo of the *J. monosperma* samples probably weakened their relationship between spectra and water status because of the relatively lower signal to noise ratio.

4.3. Needle-level spectral sensing of conifer foliar water status

Our results demonstrate the potential to spectrally estimate foliar water status in conifers at the needle level. We document significant spectral relationships for both foliar water content and water potential for two conifer species. Our results extend previous work, largely on broadleaf plants, to co-dominating conifer species of semi-arid woodlands that are undergoing drought conditions severe enough to lead to extensive tree mortality. Landscape-scale mortality of conifers in semiarid woodlands and forests indeed can be important for shifting ecosystem dynamics and functional characteristics (Allen & Bre-shears, 1998). Our results suggest that it may be possible to detect trees undergoing strong water stress and that this relationship can be correlated with water potential at the landscape scale. It is important to relate remotely sensed indices to water potential because many ecological models use this variable as an input.

More generally, and perhaps more importantly, the fact that we found relationships for both conifer species offers promise for extending these relationships to other conifer species undergoing less extreme water stress conditions. Other challenges remain to link the needle level analyses to landscape scales, including additional consideration of how to minimize the effects of canopy geometry and to address multi-species mixing. Our results, documenting relationships between two key indices of plant water condition in conifers—water content and water potential—with one to four indices obtainable from remote sensing contribute to the development of future landscape-scale metrics of plant physiology and ecosystem function and dynamics.

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