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Linking physiological responses, chlorophyll fluorescence and hyperspectral imagery to detect salinity stress using the physiological reflectance index in the coastal shrub, *Myrica cerifera*

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1. Introduction

Salinity, drought, high irradiance and high temperatures are among many factors that influence the ecophysiology of plants in coastal ecosystems and place severe limits on plant growth (Ehrenfeld, 1990). On barrier islands, salinity is considered to be the primary environmental factor influencing community patterns (Ehrenfeld, 1990; Oosting & Billings, 1942; Stalter & Odum, 1993). With predicted changes due to climate change, such as rising sea level and increases in storm intensity and frequency (Gregory & Oerlemans, 1998; Zhang et al., 2000), plant distribution on barrier islands is likely to be affected. Coastal communities are particularly sensitive to periodic, short-term flooding due to storms and hurricanes (Young et al., 1995). Aspect and distance from the shoreline strongly influence the effect of salinity on plants, thus spatial variation in salinity stress may occur across a coastal landscape (Ehrenfeld, 1990; Young et al., 1995). Early

identification of stressed areas will allow for predictions of changes in community structure across the landscape.

Characteristics of plant stress can be measured independently using reflectance or fluorescence remote sensing which provides rapid and non-destructive measurements (Anderson & Perry, 1996). Remote sensing has been useful in predicting changes in the structure and function of various ecosystems. Many studies have applied various spectrally derived indices to monitor changes in biomass (via changes in the normalized difference vegetation index, NDVI; Rouse et al., 1974), pigment composition (e.g. chlorophylls and carotenoids; Gitelson & Merzlyak, 1996), photosynthetic efficiency (determined by xanthophyll pigments, Gamon et al., 1992; Peñuelas et al., 1995), water status (Evain et al., 2004; Filella et al., 2004; Suárez et al., 2008), and multiple kinds of stress (Carter, 1994). There is a need to examine the usefulness of different reflectance indices in every community for landscape-level application (Filella et al., 2004) as some indices suitable for certain communities may not apply to others (Blackburn & Steele, 1999), or some indices used to monitor one type of stress may not apply to other types of stress (e.g. nitrogen and water stress, Peñuelas et al., 1994). Landscape-level application of reflectance indices may allow for the

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monitoring and evaluation of the health of plant communities in response to global environmental change (Filella et al., 2004).

Under conditions of stress (e.g. salinity, drought, flooding), plants are often exposed to more radiant energy than is needed for photosynthesis. The mechanisms for disposing of excess energy are limited, manifesting changes within the photosystem as a function of fluorescence and heat dissipation. Reversible declines in photosynthesis are generally accompanied by an increase in non-radiative energy dissipation mediated by the xanthophyll cycle, which protects the photosystem against permanent damage (Demmig-Adams & Adams, 1996). Changes in the epoxidation state of the xanthophyll cycle pigments and the accumulation of zeaxanthin are reflected by absorbance changes in the green region around 531–535 nm (Bilger et al., 1989; Gamon et al., 1990; Ruban et al., 1993). The amount of zeaxanthin formed is correlated with the rate of dissipation of excess energy as heat (Demmig-Adams et al., 1989). This dissipation energy can be estimated using chlorophyll fluorescence (Demmig-Adams et al., 1996). In addition, the physiological reflectance index (PRI, the reflectance at 531 nm relative to a reference wavelength) is linked to the xanthophyll cycle and may provide a non-destructive tool for the optical study of photosynthetic function (Gamon et al., 1992; Peñuelas et al., 1995). Because PRI is sensitive to xanthophyll cycle activity, it is inversely related to photosynthetic light-use efficiency (LUE; Gamon et al., 1990, 1992; Peñuelas et al., 1995).

Relationships between chlorophyll fluorescence and PRI have been demonstrated under conditions of salinity stress (Naumann et al., 2008) and water stress at the leaf-level (Dobrowski et al., 2005; Evain et al., 2004; Winkel et al., 2002), and canopy level (Evain et al., 2004; Suárez et al., 2008). Despite these successful applications of PRI, applications at spatial scales larger than the leaf require attention to the confounding effects of canopy structure (Peñuelas et al., 1995). Light-adapted measurements of chlorophyll fluorescence promote rapid detection of stress and can be easily applied beyond the leaf-level. Early detection by

remote sensing could identify plant stress at larger spatial and temporal scales, before visible effects are apparent (Cavender-Bares & Bazzaz, 2004; Helmuth et al., 2005; Zarco-Tejada et al., 2002).

Species that form monotypic canopies naturally facilitate scaling up beyond the leaf level, and have been used in many agricultural studies (Flexas et al., 2000; Gamon et al., 1990; Zarco-Tejada et al., 2003). *Myrica cerifera* is the dominant species of woody vegetation on many Atlantic barrier islands and forms dense, monospecific thickets (Ehrenfeld, 1990). *Myrica* thickets have LAI values that exceed most temperate woody communities (Brantley & Young, 2007), above the values at which PRI becomes insensitive to the background effect of the soil (Barton & North, 2001), reducing the confounding effects of canopy structure. Thus, *M. cerifera* may be a model species for scaling up in natural ecosystems. Laboratory studies of *M. cerifera* showed decreases in light-adapted chlorophyll fluorescence and subsequent increases in non-photochemical quenching under salinity and drought stress, indicating the possibility of xanthophyll-cycle dependent energy dissipation, and thus may enable rapid stress detection at the canopy level (Naumann et al., 2007).

We evaluated the effect of natural salinity and drought stress on plant physiological status, chlorophyll fluorescence, canopy-level fluorescence and airborne hyperspectral reflectance of *Myrica cerifera* located on a barrier island of the Atlantic Coast. Specific objectives were to (1) determine whether chlorophyll fluorescence could be used to detect salinity and drought stress in the field, (2) determine if chlorophyll fluorescence is related to plant physiological status, (3) relate canopy-level hyperspectral reflectance to chlorophyll fluorescence, and (4) use airborne remote sensing reflectance data to algorithmically identify stress at the landscape-level. Through monitoring areas of stress and understanding specific physiological responses, we may be able to predict changes in plant dominance and community structure (Filella et al., 1998).

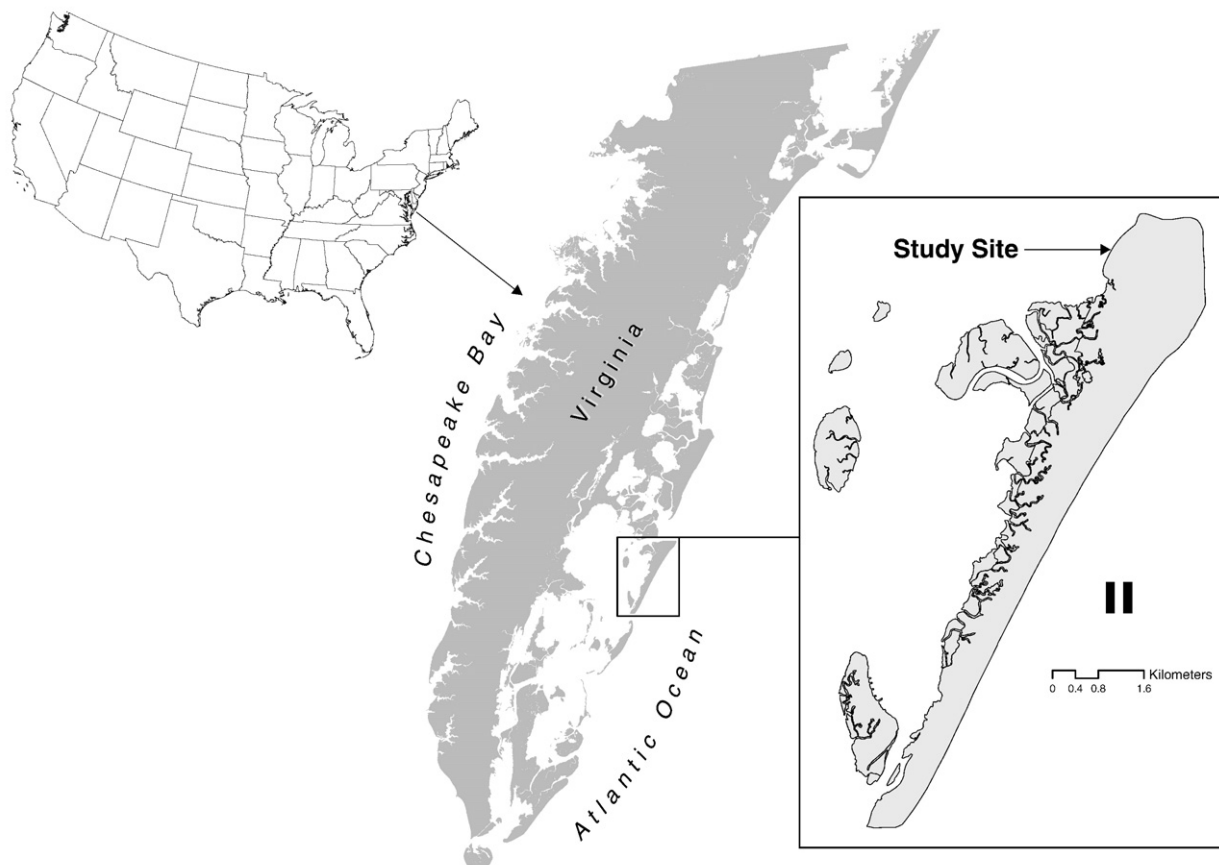


Fig. 1. Location map for study sites at Hog Island, Virginia.

2. Methods

2.1. Study site

The study was conducted on the North end of Hog Island (37° 40'N; 75° 40'W), a barrier island located on the Eastern Shore of Virginia, from June to October 2007 (Fig. 1). On Hog Island, four existing thickets represent a range of successional stages. The oceanside, northern end of the island has been accreting approximately 5 m/year for 140 years (Hayden et al., 1991), resulting in a parallel series of dunes and swales. The mesic swales are dominated by *Myrica cerifera* L. (Myricaceae), an evergreen, nitrogen-fixing, salt sensitive shrub (Ehrenfeld, 1990; Young, 1992). We conducted our study in two experimental sites of the easternmost thicket, which lies 200 m from the shoreline, and contains patches of young shrubs (~10 years old). The thicket is ~32 m in width and 197 m long. Measurements were taken from the oceanside of the thicket, which is exposed to sea spray, and from the protected, leeside of the thicket.

2.2. Physiological measurements

Daily variations in air temperature and precipitation were obtained from a meteorological station on Hog Island (Krovetz et al., 2007). Measurements of stomatal conductance, leaf net photosynthesis, leaf fluorescence, relative water content, and tissue chlorides were collected monthly at mid-day (1000–1400 h) on the fourth or fifth

fully expanded sunlit leaf of each plant. New leaf growth begins in early May and continues until mid-September. We randomly selected five individual shrubs, and made 2 measurements per individual ($n=10$) for each sampling date. The same leaves were used for each measurement on a given day. Separate leaves were used for tissue chlorides due to destructive sampling during measurements of relative water content. Stomatal conductance (g_{wv}) and leaf net photosynthesis (A_{Net}) were measured using a portable infrared gas analyzer (LI- 6200, LI-COR, Inc., Lincoln, NE).

Light-adapted measurements of chlorophyll fluorescence were conducted using a pulse amplitude modulated leaf fluorometer (PAM-2000, Walz, Effeltrich, Germany). The relationship between maximal fluorescence in a light-adapted leaf after a saturating pulse of light (F'_m) and steady-state fluorescence prior to any saturating pulse (F_s) was used to estimate the effective quantum yield of photosystem II:

$$\Delta F/F'_m = [F'_m - F_s]/F'_m$$

After gas exchange and fluorescence measurements, leaves were clipped at the stem and kept at 100% humidity. Relative water content was measured as:

$$RWC(\%) = (FW - DW)/(SFW - DW) * 100$$

where FW is fresh weight, DW is dry weight, and SFW is saturated fresh weight of the leaves after re-hydrating samples for 24 h (Turner, 1981). Tissue chlorides were quantified for leaves collected adjacent to

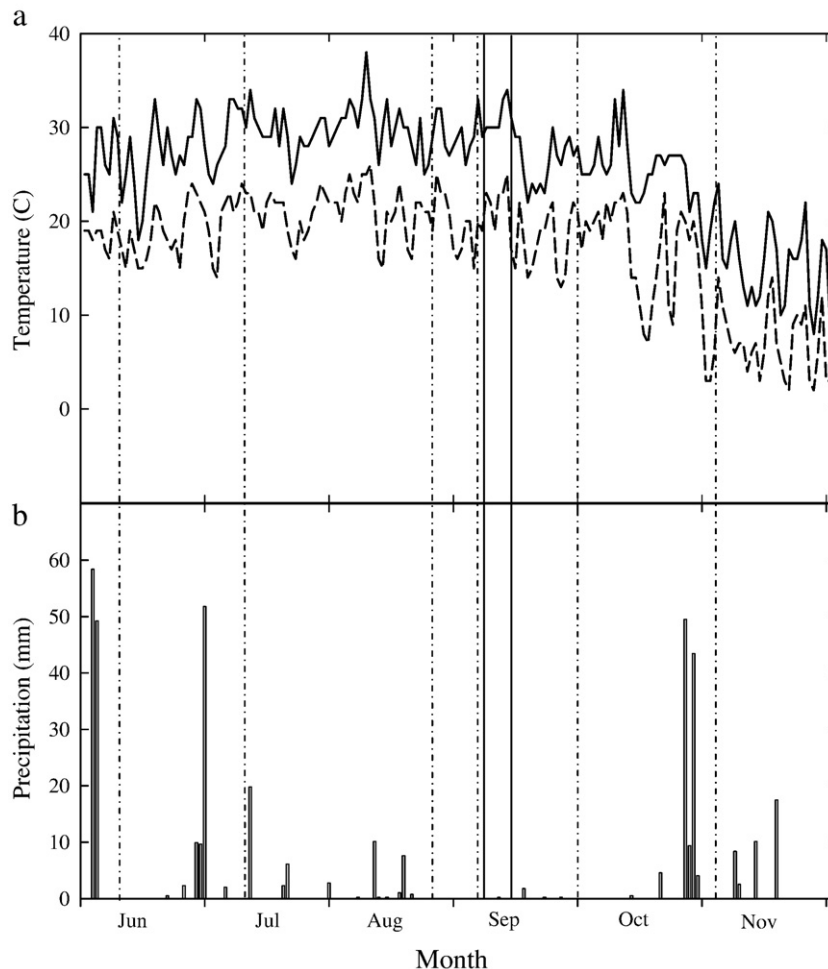


Fig. 2. (a) Monthly variations in maximum (solid line) and minimum temperature (dotted line) as measured from a meteorological station on Hog Island between June 1 and November 30, 2007. (b) Monthly variation in precipitation on Hog Island. Dashed lines indicate the monthly sampling dates for physiological measurements. Solid lines indicate the September 6 date for canopy-level reflectance measurements and the September 13 date for airborne-level reflectance acquisition.

Table 1
ANOVA results for selected variables and reflectance indices

Variable	F	P
g_{wv}		
Site	24.43	<0.001
Month	38.10	<0.001
Month x site	4.39	0.0011
A_{net}		
Site	45.83	<0.001
Month	79.99	<0.001
Month x site	10.48	<0.001
RWC		
Site	3.21	0.0758
Month	14.27	<0.001
Month x site	1.33	0.2559
Tissue chlorides		
Site	394.62	<0.001
Month	0.69	0.6319
Month x site	0.47	0.7989
$\Delta F/F_m$		
Site	51.36	<0.001
Month	0.28	0.9208
Month x site	1.53	0.1868
Canopy-level		
PRI	6.31	0.0457
NDVI	0.18	0.6834
CI	0.00	0.9641
WBI	0.05	0.8329
Landscape-level		
PRI	114.22	<0.001
NDVI	0.71	0.4011
CI	2.96	0.0870
WBI	10.90	0.0011

P-values in bold denote significance at $\alpha=0.05$.

those used for physiological measurements ($n=10$). Leaf samples were oven-dried at 80 °C for 72 h and then ground in a fine mesh mill. For each sample, 0.5 g of material was placed in a tube with 40-mL of deionized water. Samples were placed in a boiling water bath for 2 h,

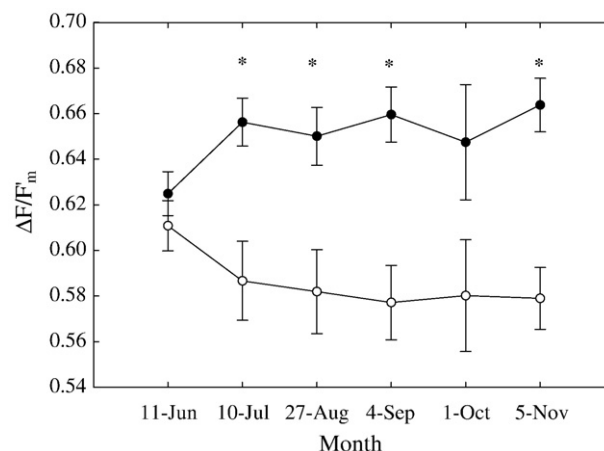


Fig. 4. Monthly variations in $\Delta F/F_m$ on the backside (filled symbols) and oceanside (open symbols) of the *Myrica cerifera* thicket. Values represent means ± 1 standard error. An * represents statistical differences between sites in a given month.

cooled, and filtered into 100-mL volumetric flasks. To each sample, 2-mL of 5 M NaNO_3 was added as an ionic equalizer, and then samples were brought to volume with deionized water (Young et al., 1994). Chloride levels were determined using a chloride electrode (model 9617b, Orion, Boston, MA).

2.3. Canopy hyperspectral measurements

Canopy spectral reflectance (350–2500 nm) was measured at four sites on each side of the thicket ($n=8$) on September 6, 2007 using an ASD FieldSpec Pro Full Range reflectance radiometer (Analytical Spectral Devices, Inc., Boulder, CO). The ASD spectral resolution is ~1 to 3 nm from the visible to the short-wave infrared. The fore-optic of the radiometer was held from a tall pole in a nadir

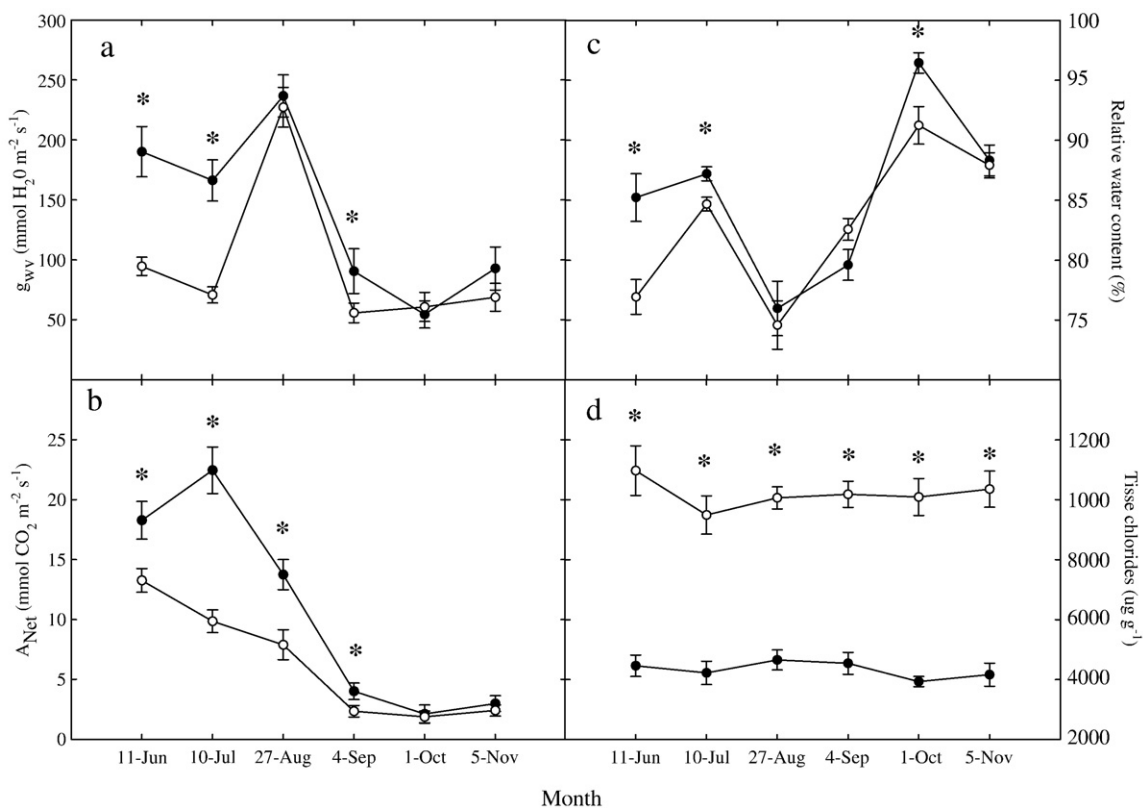


Fig. 3. (a) Monthly variations in stomatal conductance, (b) net photosynthesis, (c) relative water content and (d) tissue chlorides on the backside (filled symbols) and oceanside (open symbols) of the *Myrica cerifera* thicket. Values represent means ± 1 standard error. An * represents statistical differences between sites in a given month.

position at a distance ~1 m above the canopy using an 8° field-of-view on a cloudless day. To acquire a representative value, multiple spectra were collected around solar noon and averaged for each site. Data were reduced from binary using the manufacturer's software. Reflectance spectra were calculated by dividing the spectral radiance of the canopy by a NIST Spectralon reflectance standard. A reference measurement from the standard was taken before each canopy measurement. This standard provides a near 100% lambertian reflectance surface for calibration. Using the resulting reflectance values, several canopy reflectance indices were calculated as follows:

Physiological Reflectance Index (Gamon et al., 1992)

$$PRI = (\rho_{531} - \rho_{570}) / (\rho_{531} + \rho_{570})$$

Normalized Difference Vegetation Index (Rouse et al., 1974)

$$NDVI = (\rho_{800} - \rho_{670}) / (\rho_{800} + \rho_{670})$$

Chlorophyll Index (Gitelson & Merzlyak, 1994, 1996)

$$CI = (\rho_{750} - \rho_{705}) / (\rho_{750} + \rho_{705})$$

Water Band Index (Peñuelas et al., 1993)

$$WBI = \rho_{970} / \rho_{900}$$

Concurrent measurements of $\Delta F/F_m$ were made on 50 leaves at each site with a pulse amplitude modulated leaf fluorometer (PAM-2000, Walz, Effeltrich, Germany) to represent canopy fluorescence.

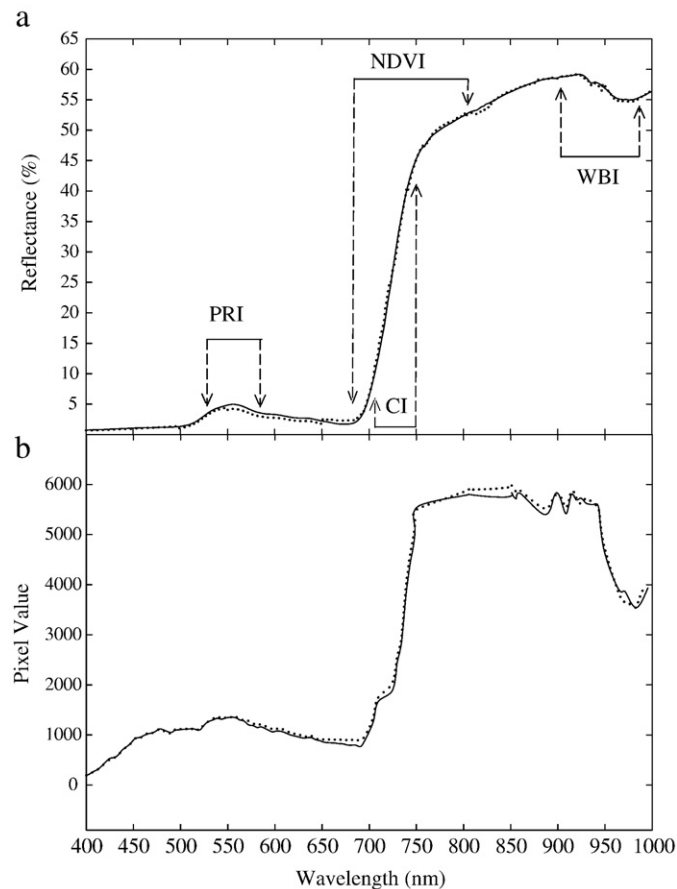


Fig. 5. Representative reflectance spectra showing spectral regions used in the calculations of hyperspectral indices from (a) canopy-level measurements and (b) airborne-level imagery. The solid lines represent the backside site and the dotted lines represent the oceanside of the thicket.

Table 2

Linear regression results for selected independent variables (i.v.) and dependent variables (d.v.)

i.v.	d.v.	r^2	F	P
$\Delta F/F_m$	PRI	0.69	13.74	0.0100
$\Delta F/F_m$	NDVI	0.01	0.06	0.8131
$\Delta F/F_m$	CI	0.01	0.06	0.8206
$\Delta F/F_m$	WBI	0.00	0.01	0.9407
Canopy-level				
PRI	NDVI	0.01	0.06	0.8098
Landscape-level				
PRI	NDVI	0.04	9.29	0.0026

P -values in bold denote significance at $\alpha=0.05$.

2.4. Airborne image acquisition

An airborne hyperspectral mission was flown concurrent with the physiological and canopy reflectance measurements at Hog Island on September 13, 2007. Hyperspectral data (3 nm resolution) were provided by the SpectIR using the ProSpecTIR VIS hyperspectral imaging spectrometer (SpectIR Corp.). Hyperspectral imagery covering 450 nm to 2450 nm was collected under cloud-free conditions at 1700 m (AGL) providing a data set representing 2 m/pixel on the ground and a final spectral cube 356 bands deep. These data products were post-processed to correct for geometric and radiometric (e.g., bi-directional) effects. Ground reflectance radiometry was used to calibrate the data based on target endmembers collected in-scene with the ASD reflectance radiometer. This effectively placed the scene into reflectance units and helped to negate any atmospheric effects. Calibration was performed using the empirical line calibration method within ENVI (RSI, Inc.). One hundred points/pixels were randomly selected from both the backside and oceanside sites sampled and the corresponding spectra extracted. The extraction of pixels with 2 m resolution enabled the calculation of indices without any shadowing effects. Landscape-level reflectance indices were calculated as follows:

$PRI = (\rho_{30} - \rho_{39}) / (\rho_{30} + \rho_{39})$ where ρ_{30} is the reflectance band centered at 529 nm and ρ_{39} is reflectance centered at 572 nm

$NDVI = (\rho_{87} - \rho_{60}) / (\rho_{87} + \rho_{60})$ where ρ_{87} is the reflectance centered at 802 nm and ρ_{60} is the reflectance centered at 672 nm

$CI = (\rho_{76} - \rho_{67}) / (\rho_{750} + \rho_{705})$ where ρ_{76} is the reflectance centered at 749 nm and ρ_{67} is the reflectance centered at 705 nm

$WBI = \rho_{120} / \rho_{107}$ where ρ_{120} is the reflectance centered at 970 nm and ρ_{107} is the reflectance centered at 900 nm.

2.5. Statistical analyses

Two-way analysis of variance was used to test for variations in month and site for the following measurements: stomatal conductance, photosynthesis, chlorophyll fluorescence, relative water content and tissue chlorides (Zar, 1999). Significant differences among months were identified with Tukey tests ($\alpha=0.05$). Differences in PRI, NDVI, CI, and WBI between sites were tested using the t -test. Variations in reflectance indices were related to variations in chlorophyll fluorescence using linear regressions.

3. Results

3.1. Leaf-level physiological measurements

The summer of 2007 was unusually dry and characterized by a persistent drought (Fig. 2). Except for August 8, maximum temperatures were close to the 30 year average (30 °C) and did not go above those reported for optimal photosynthesis in *M. cerifera* (Young, 1992). Precipitation was concentrated in June and early July. Only 2 rain

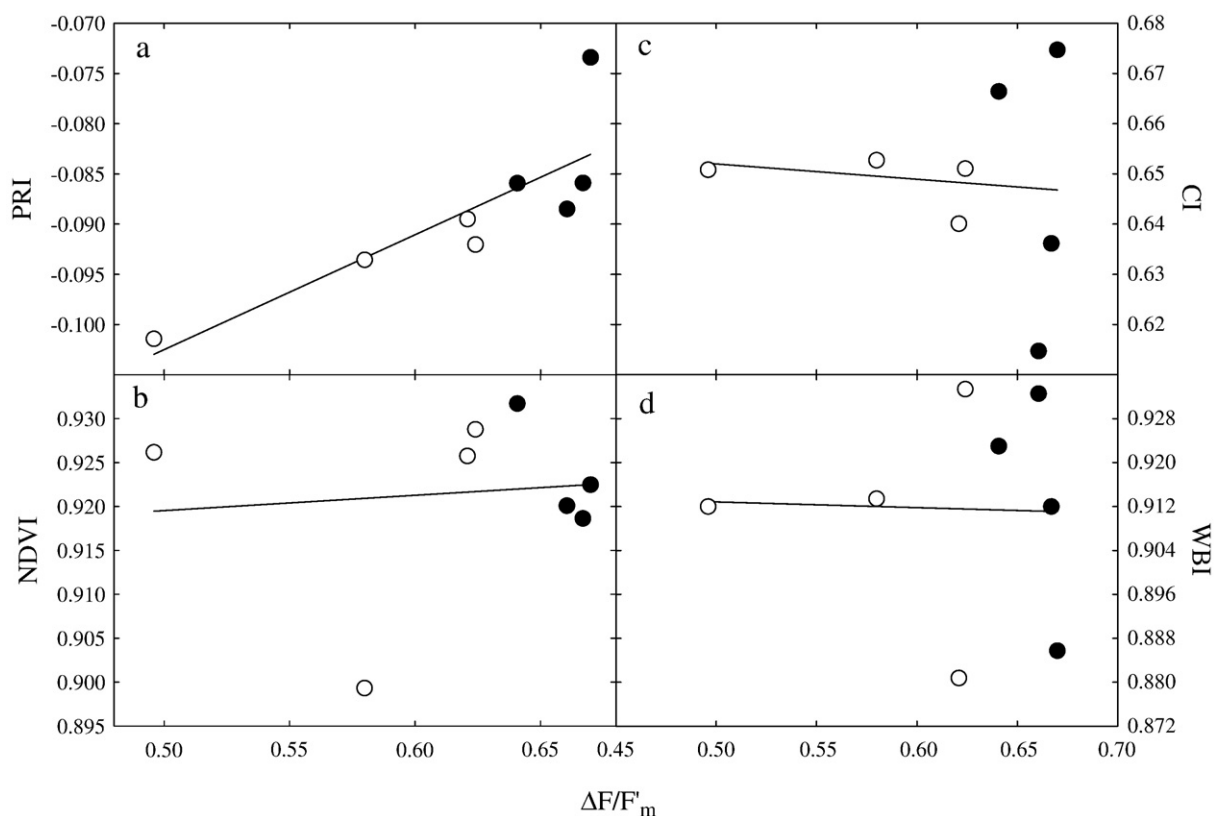


Fig. 6. (a) Relationships obtained between PRI, (b) NDVI, (c) CI, and (d) WBI with $\Delta F/F'_m$ on the backside (filled symbols) and oceanside (open symbols) of the *Myrica cerifera* thicket. Indices were obtained from canopy-level reflectance data.

events >5 mm occurred after July 11 and very little precipitation occurred after mid-August (Fig. 2). Precipitation for June through September was 39% below the 30 year average (388 mm).

Stomatal conductance and net photosynthetic rates were highest on the backside of the thicket throughout the summer (Table 1, Fig. 3).

There were significant differences between months for stomatal conductance and photosynthesis, as well as significant interactions between site and month (Table 1). The highest rates of stomatal conductance occurred in August for both the backside and oceanside sites (236 ± 17 and 227 ± 16 mmol $\text{H}_2\text{O m}^{-2} \text{s}^{-1}$, respectively; Fig. 3),

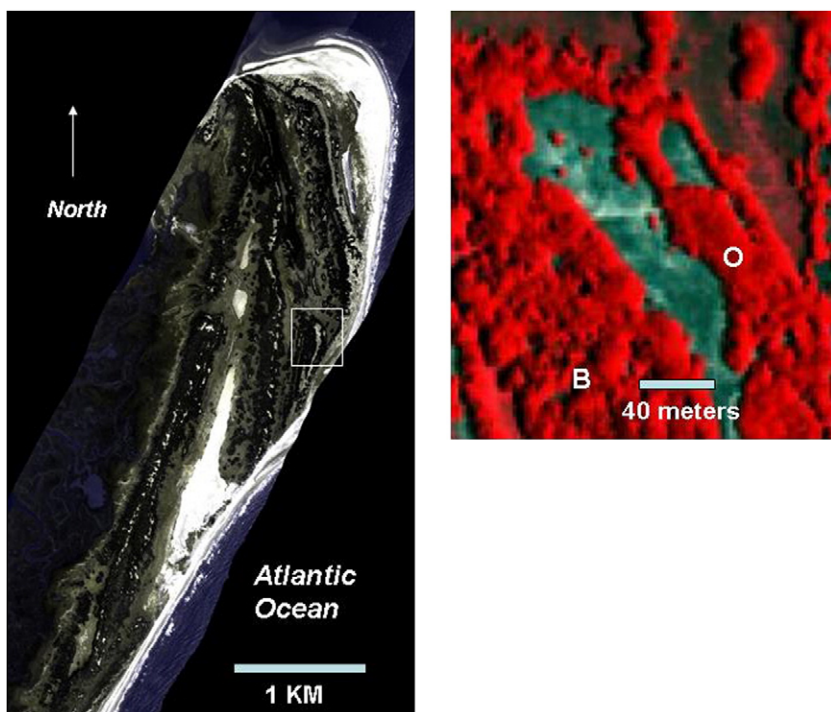


Fig. 7. SpectIR hyperspectral images of Hog Island and the study sites used. O = oceanside and B = backside sites. False color composite uses bands 802 nm, 672 nm, and 529 nm (RGB).

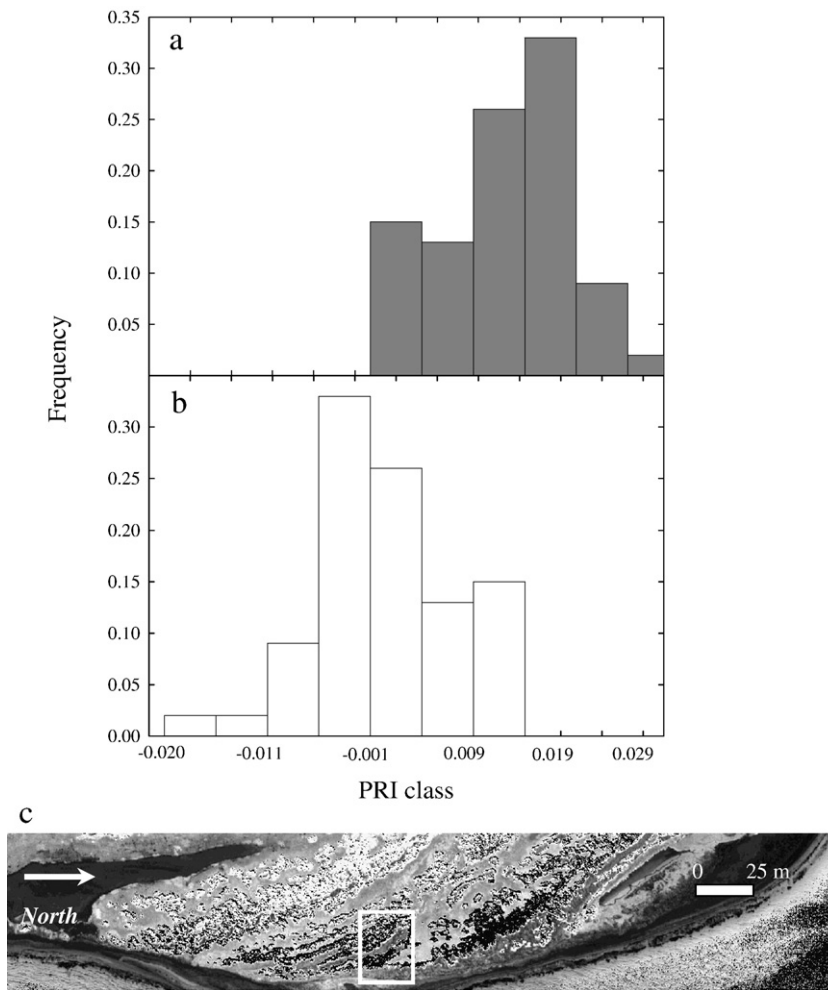


Fig. 8. Frequency histograms of PRI values obtained from hyperspectral image data on the (a) backside and (b) oceanside of the *Myrica cerifera* thicket and (c) computed PRI resultant images for SpectIR hyperspectral data using bands 30 (529 nm) and 39 (572 nm). The square highlights the study area.

which followed a few rain episodes in the prior week. The highest rates of net photosynthesis occurred in June ($13.3 \pm 0.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on the oceanside of the thicket, with rates declining each month thereafter. Net photosynthesis was highest in July on the backside of the thicket ($22.5 \pm 1.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Despite high values of stomatal conductance, rates of photosynthesis decreased in August. The lowest values of stomatal conductance and photosynthesis were reached in October for both the backside ($54 \pm 11 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, $2 \pm 1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and oceanside ($61 \pm 12 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, $2 \pm 1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

Seasonal patterns of relative water content did not reflect the late summer drought. Relative water content was significantly different over time but did not differ significantly between sites, and there was no interaction between sites and month (Table 1). The lowest values of relative water content occurred in August, when stomatal conductance was high for both the backside ($76 \pm 2\%$) and the oceanside ($74 \pm 2\%$) sites (Fig. 3). Both the oceanside and backside of the thicket experienced partial stomatal closure after August, allowing relative water contents to increase (Fig. 3). By October, relative water content was $>90\%$ for both sites ($96 \pm 1\%$ backside, $91 \pm 2\%$ oceanside). Total chlorides present in leaves were higher on the oceanside ($10193 \pm 403 \mu\text{g g}^{-1}$) compared to the backside ($4329 \pm 200 \mu\text{g g}^{-1}$; Fig. 3). There was no significant difference among months and there was no significant interaction between month and site (Table 1).

Despite the unusually dry summer, there was no significant change in $\Delta F/F_m$ from one month to the next. $\Delta F/F_m$ did differ by site, and

was significantly lower on the oceanside site compared to the backside throughout the summer (Table 1; Fig. 4). Values averaged around 0.64 on the backside and 0.58 on the oceanside.

3.2. Canopy-level reflectance

Spectral reflectance data were collected under sunny and cloud-free conditions. Air temperature was 31°C , with relative humidity of 44% and $1944 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD at solar noon. There were subtle differences in both the canopy-level and airborne-level reflectance spectra between the two sites, particularly in the 525–700 nm range (Fig. 5). PRI was positively related to $\Delta F/F_m$ (Table 2). PRI decreased from -0.07 to -0.10 , while $\Delta F/F_m$ decreased from 0.67 to 0.49, with higher $\Delta F/F_m$ occurring on the backside of the thicket (Fig. 6). PRI was significantly lower on the oceanside (Table 1). NDVI was not related with $\Delta F/F_m$ (Table 2; Fig. 6). NDVI values ranged from 0.90 to 0.93 and did not differ between sites (Table 1). There were no significant relationships between CI and $\Delta F/F_m$ (Table 2). WBI was not related to $\Delta F/F_m$ (Table 2; Fig. 6). WBI ranged from 0.88 to 0.93, and there was no significant difference between sites (Table 1). PRI was not significantly related to NDVI (Table 2), suggesting that the indices are independent and that PRI is not tracking changes in NDVI.

3.3. Landscape-level airborne reflectance

On the day of the flight, air temperature was 29°C , with relative humidity of 45% and $2076 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD at solar noon. Oceanside

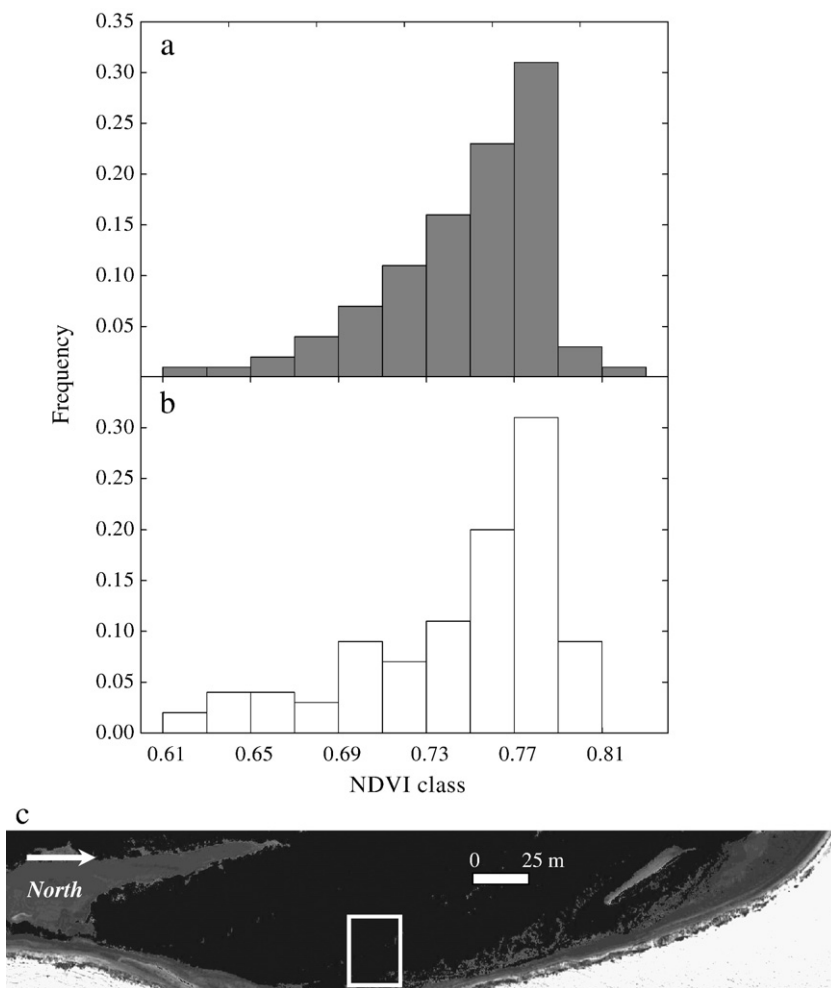


Fig. 9. Frequency histograms of NDVI values obtained from airborne hyperspectral image data on the (a) backside and (b) oceanside of the *Myrica cerifera* thicket and (c) computed NDVI resultant images for SpectIR hyperspectral data using bands 87 (802 nm) and 60 (672 nm). The square highlights the study area.

and backside study sites used in physiological measurements were employed for landscape-level determination of PRI (Fig. 7). At the landscape-level, PRI was higher on the backside sites relative to the oceanside. Frequency histograms of pixels in different size classes showed that the distribution of PRI was shifted to the right on the backside of the thicket relative to the oceanside, although there was some overlap between sites (Fig. 8). Average values of PRI were 0.009 on the backside and -0.003 on the oceanside and the difference was significant (Table 1). 69% of the sites on the oceanside had values of PRI lower than 0, compared to only 15% of the sites on the backside of the thicket. NDVI did not differ between the two sites and averaged 0.73 (Table 1; Fig. 9). CI was not significantly different between the two sites (Table 1; Fig. 10). There was a significant difference in WBI between sites (Table 1); however, frequency histograms of pixels in different size classes revealed that both sites approximated normal distributions and values of WBI spanned the same range (Fig. 10). There was a significant, but weak relationship between PRI and NDVI (Table 2; Fig. 11), again suggesting that the indices are independent of one another.

4. Discussion

Because *M. cerifera* occurs in coastal environments, it must withstand periods of drought and episodic flooding with saltwater in the presence of high irradiances. The summer of 2007 was extremely dry with little rainfall occurring after mid-July. Young

(1992) showed that *M. cerifera* is sensitive to moisture stress, with partial stomatal closure occurring at a leaf water potential of -0.8 MPa. This sensitivity to water stress was observed in the field where partial stomatal closure was observed after relative water content reached very low values. Values of stomatal conductance during the summer were lower than those reported by Young (1992; approximately $400 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) probably due to drought conditions. Rates of photosynthesis were also slightly lower compared to those in an unusually wet July (approximately $32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Young, 1992). Drought induced stress was apparent in CO_2 assimilation and relative water content by August, despite high values of stomatal conductance. Although stomatal conductance was high, photosynthesis continued to decline. The reasons for this are unclear, however, non-stomatal limitations to photosynthesis could potentially explain this anomaly if stomatal conductance values had been higher in the morning (Flexas & Medrano, 2002). After August, stomatal conductance and photosynthetic rates continued to remain very low through November. Relative water content values increased in September, despite the lack of significant rain events. This may be partially explained by the increase in leaf fall that begins in late August and peaks in November, thereby reducing water demand (Brantley & Young, 2008). For any physiological parameter measured, there is both a seasonal response and a diurnal response. Measurements taken at one point during the day may be confounded by the changes in both the seasonal and diurnal patterns. To fully understand the patterns of stomatal conductance, photosynthesis and relative water content seen

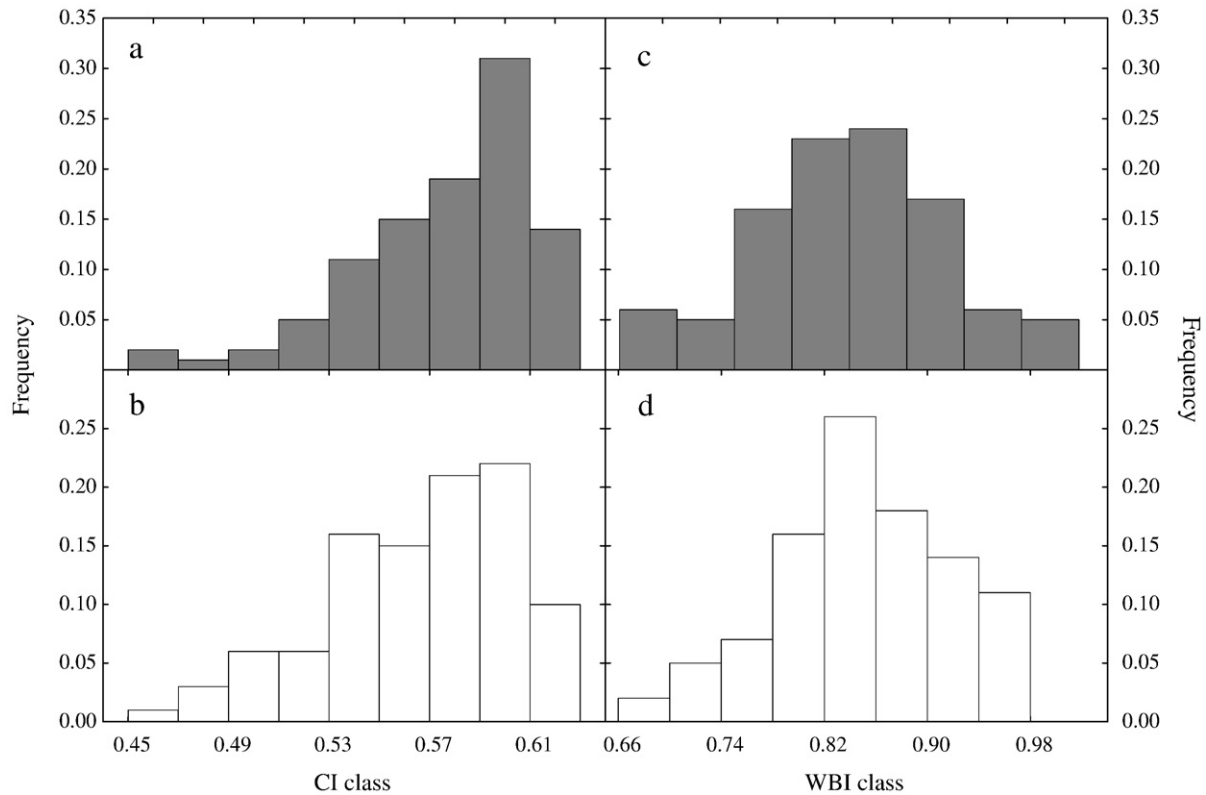


Fig. 10. Frequency histograms of CI values obtained from airborne hyperspectral image data on the (a) backside and (b) oceanside of the *Myrica cerifera* thicket. Frequency histograms of WBI values obtained from airborne hyperspectral image data on the (a) backside and (b) oceanside of the *Myrica cerifera* thicket.

in this study, further investigation into diurnal patterns of physiological responses to stress is needed.

Depressions in CO_2 assimilation due to stress are generally associated with stomatal closure, which also reduces water loss (Pereira & Chaves, 1993). Partial stomatal closure was observed by September, and this likely accounted for low photosynthetic rates at both sites. Under conditions of mild water stress, photosynthesis may be inhibited through ATP limitation not CO_2 diffusion (Tezara et al., 1999). Leaf relative water content was very low during August, and may have contributed to declining rates of photosynthesis, even though stomatal conductance values were at the highest rates recorded during the study. Temperatures during the study were

near optimum for photosynthesis ($\sim 30^\circ\text{C}$) and likely did not inhibit CO_2 assimilation (Young, 1992).

Drought did not induce changes in $\Delta F/F_m$ in the field. This was unexpected considering the low values of CO_2 assimilation and that declines in $\Delta F/F_m$ occurred in *M. cerifera* after 2 days of drought stress in lab studies (Naumann et al., 2007). Differences in chlorophyll fluorescence between the two sites were likely due to salinity effects. Values were consistently lower on the exposed oceanside site, which also exhibited higher leaf tissue chlorides. Salinity may also be responsible for lower values of stomatal conductance, photosynthesis, and relative water content on the oceanside site (Naumann et al., 2007, 2008).

One mechanism that has evolved as a means of safely dissipating excess light to avoid photoinhibition and photooxidation involves changes in pigments of the xanthophyll cycle. The rate of dissipation of excess energy as heat is correlated with the amount of zeaxanthin present (Demmig-Adams et al., 1989). In some species, PRI has been demonstrated to be a reliable indicator of plant stress, more so than chlorophyll-based indices (Richardson et al., 2001; Thorhaug et al., 2006) because of rapid changes in xanthophyll cycle pigments. However, this is not true in all species (Carter, 1998; Estep & Carter, 2005), making it necessary to examine the efficacy of reflectance indices in different canopies (Filella et al., 2004). $\Delta F/F_m$ is an indicator of the actual Photosystem II (PSII) efficiency in light (Ball, 1994). Significant relationships have been identified between PRI and $\Delta F/F_m$ under conditions of drought stress (Evain et al., 2004), saltwater flooding (Naumann et al., 2008), and over a range of irradiance levels (M  thy, 2000). Our results showed a positive, linear relationship at the canopy-level between $\Delta F/F_m$ and PRI, providing evidence for the utility of using PRI to estimate changes in fluorescence under conditions of salinity stress.

Spatial variations in canopy-level PRI may be an indication of variations in xanthophyll cycle pigments between plants with different capacities for photosynthetic efficiency (Nichol et al.,

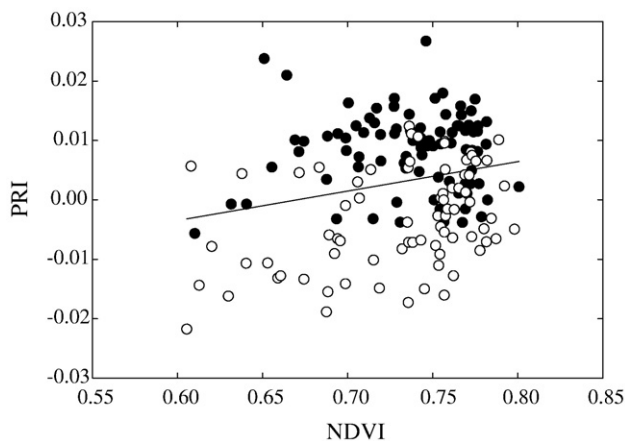


Fig. 11. Relationship between PRI and NDVI on the backside (filled symbols) and oceanside (open symbols) of the *Myrica cerifera* thicket. Indices were obtained from airborne hyperspectral image data.

2006). Higher PRI values on the backside of the thicket indicated a higher xanthophyll epoxidation state and may be a reflection of the increased photosynthetic rates seen on the backside relative to the oceanside site. Changes in PRI between the two sites at both the canopy-level and landscape-level were likely due to salinity stress more so than water stress. Leaf tissue chlorides were much higher on the oceanside site, with corresponding lower PRI values, while relative water content and WBI did not differ significantly between the two sites. These results suggest that PRI is able to track spectral changes in salinity stress as evidenced by differences in chlorophyll fluorescence and tissue chlorides. Thorhaug et al. (2006) demonstrated changes due to salinity in spectral reflectance indices in seagrass, especially PRI, that were consistent with stress responses in terrestrial plants. Our results support the possibility of using PRI at larger spatial scales. Currently, the spaceborne Earth Observing-1 (EO-1) Hyperion satellite sensor is available for mapping PRI over large geographic areas. It has been successfully used to monitor physiological and biochemical changes due to chronic water stress (Asner et al., 2004) and to assess photosynthetic LUE in rainforests under various precipitation and substrate conditions (Asner et al., 2005). A MODIS-derived PRI has also been correlated to ecosystem-level LUE, but with limited success and reduced spatial resolution (Drolet et al., 2005).

Soil background and canopy LAI must be accounted for when using PRI to detect water stress (Suárez et al., 2008). In our study, LAI of the shrub thicket was estimated to be 10, with very little to no variation among sites ranging from the backside to the oceanside sites, which was reflected in NDVI values (Brantley & Young, 2007). Values of LAI above 6 are insensitive to the background effect of the soil, eliminating soil background as a confounding factor (Barton & North, 2001). The lack of relationship between PRI and NDVI at both the canopy and landscape level suggests that issues related to structure and viewing geometry were not a factor affecting the PRI signal. PRI can be scaled from upper canopy leaves to the whole-plant canopy (Stylinski et al., 2002). Due to the aforementioned factors, *M. cerifera* thickets are ideal for stress detection and scaling-up to the landscape level.

5. Conclusions

Drought stress was evident in late summer, as seen in low photosynthetic rates and stomatal closure. Despite the pronounced drought, values for chlorophyll fluorescence did not change, indicating that *M. cerifera* is able to effectively dissipate excess light even in times of stress. While drought effects were not measurable via fluorescence, salinity stress did cause lower values of $\Delta F/F_m$ on the oceanside sites. Rates of CO₂ assimilation and stomatal conductance were also lower on the oceanside, also attributed to salinity stress. Few studies have examined the suitability of different reflectance indices for plants growing naturally in the field (Filella et al., 2004). In this study, ground-based canopy reflectance showed good correlation between PRI and chlorophyll fluorescence. Changes in both PRI and fluorescence were attributed to salinity stress. Airborne landscape-level reflectance measurements also showed lower PRI values in areas of higher salinity (i.e. oceanside sites). *M. cerifera* thickets have been expanding in many locations on the Virginia barrier islands, but this expansion has been confounded by the effects of sea-level rise and storm intensity (Young et al., 2007). Although more work is needed with many levels of salinity, our results suggest that PRI may be used to detect salinity stress due to storm overwash or groundwater intrusion and to identify areas across the landscape where community structure may change due to sea-level rise.

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