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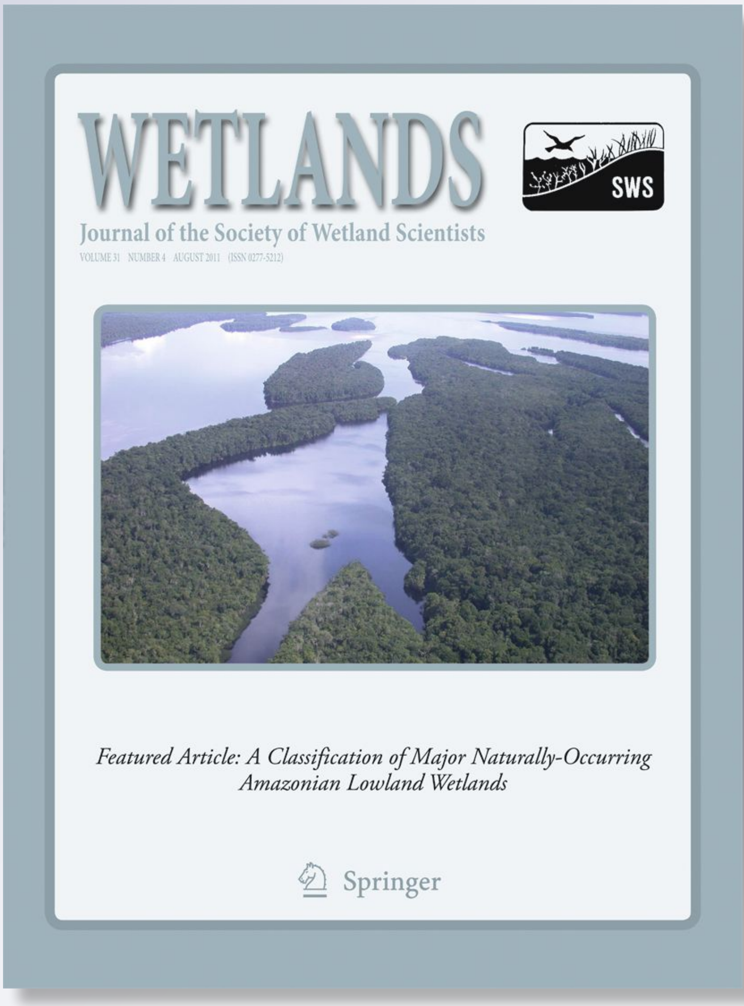

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ARTICLE

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Abstract Plant growth is one of the most important variables to measure in long-term research plots, but the negative effects of labor-intensive and destructive sampling can restrict frequent assessment of plant biomass. Here, we used field-based, active radiometry to assess plant biomass in an ongoing, experimental manipulation of atmospheric CO_2 and soil nitrogen availability in a tidal wetland. We compared the ability of several radiometric vegetation indices (VIs) to predict total plant biomass and that of two plant functional groups, sedges and grasses. All VIs estimated total biomass better in July than in October, when senescence had begun. All VIs correlated strongly and positively to grass biomass (average r=0.83) and weakly or negatively to sedge biomass (r=−0.30). Modified soil-adjusted vegetation index (MSAVI2) performed well through space (average July total biomass r=0.83) and time (across four sampling times r=0.83) and predicted CO_2 and nitrogen treatment effect sizes. In conjunction with conventional biomass measurements field-based, active radiometry provides (1) a frequent estimate of biomass that can reveal plant responses to environmental stimuli that would otherwise escape detection, and (2) a viable alternative to frequent destructive sampling for assessing growth of fine-stemmed species such as *Spartina patens* and *Distichlis spicata*.

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Introduction

Plant productivity provides energy for nearly all other life on earth. Changes in productivity of unmanaged ecosystems may have important consequences for ecosystem functions and foodwebs that depend on these inputs. Further, plant productivity is generally the largest flux of carbon into ecosystems, and any alteration thereof could drive changes in ecosystem carbon storage (Beer et al. 2010). The importance of these processes is magnified in coastal wetlands, which sustain critical oceanic foodwebs and sequester inordinate masses of carbon (Bridgham et al. 2006). Moreover, tidal wetland plants trap sediment, and their litter accumulates in anoxic soils, so wetland plant productivity plays a relatively large role in sustaining entire coastal wetland ecosystems (Langley et al. 2009a). Therefore, improving techniques to investigate how plant growth responds to both experimental treatments and natural environmental perturbations is critical to the advance of ecology generally and wetland ecology in particular (Klemas 2011).

Conventional productivity assessments are labor-intensive and destructive to sensitive, long-term research plots (Zhang et al. 1997; Chen et al. 2009). Although the vegetative structures of some species may be suitable for non-destructive, e.g. allometric biomass estimates (Morris and Haskin 1990), others must be destructively harvested to obtain accurate measures. Therefore, measurements are often made only once

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or twice a year in many manipulative, long-term field experiments (e.g. Shaw et al. 2002; Erickson et al. 2007; Gedan and Bertness 2009; Reich 2009). A shortcoming of this approach is that seasonal patterns of plant growth may vary widely from year to year (Cleland et al. 2007), particularly in the face of global change factors that alter phenological patterns of growth (Cleland et al. 2006; Taylor et al. 2008). Typically, researchers target peak biomass but lack foreknowledge of when plant biomass will peak, and thus, may substantially underestimate productivity when peak plant growth occurs before or after the prescribed sampling dates. Furthermore, interannual patterns of plant growth have been related to a variety of factors such as precipitation, temperature, salinity and inundation to reveal controls on plant productivity (Erickson et al. 2007). More frequent assessment of changes in plant growth throughout a season could greatly enhance the sensitivity of detecting such relationships *within* a growing season (Smith et al. 1998).

Use of airborne or satellite-borne imagery has accelerated in wetlands (Silva et al. 2008; Adam et al. 2010; Klemas 2011). Classification of wetlands across relatively broad ranges of vegetation classes has become increasingly sophisticated (Zhang et al. 2011), but experimentally manipulated plots on the 1-m scale are too small to reliably sample from spacecraft, and may be too expensive to assess frequently from aircraft at the appropriate spatial resolution (Smith et al. 1998; Klemas 2011). Further, long-term time series of passive reflectance may be subject to confounding changes in spectral quality arising from differences in sun angle, atmospheric visibility, or water depth among sample times (Eastwood et al. 1997; Jones 2011; Klemas 2011). Yet, frequent, nondestructive assessments of plant growth, as well as the relative effects of various experimental treatments on growth in long-term research plots could provide great value in understanding how plants respond to treatments through time, and how those responses may depend on other factors (Eastwood et al. 1997). An ideal assessment technique would be robust to the large differences in growth and foliar chemical composition incurred by the treatments as well as changes in spectral environment through time.

A new generation of simplified, handheld active radiometers has become commercially available. Active radiometry supplies a light source so that reflectance measures are independent of background variability in the light environment that can interfere with passive, field-based reflectance measurements (e.g. Penuelas et al. 1993). Active, field-based radiometry has been used extensively in agro-ecosystems to assess plant growth and nutrient status, allowing growers to tailor resource additions with great accuracy and spatial resolution, thereby reducing waste and runoff of expensive fertilizers (Biewer et al. 2009). However, field-based radiometry has proved only modestly useful in many non-agricultural ecosystems such as wetlands. While radiometry may be useful for distinguishing among cover types (Artigas and Yang 2006), nonuniformity in plant reflectance, leaf angle, and canopy height among different species may confound estimates of plant growth (Spanglet et al. 1998).

Here, we compared active, field-based radiometry to conventional biomass and productivity measurements during a global change experiment in a tidal wetland. Our goal was to assess the efficacy of using frequent radiometric measurements to track the growth of two distinct functional plant groups in response to global change manipulations across two growing seasons. Additionally, we used radiometry to relate changes in plant growth to intra-annual variability in climatic factors.

Methods

Site

This study was conducted at the Smithsonian Global Change Research Wetland in a brackish marsh on the Rhode River, a sub-estuary of Chesapeake Bay. The $CO_2 \times N$ experiment has been described previously (Langley et al. 2009a, b). Briefly, 20 octagonal, open-top chambers each enclose 3.3-m^2 plots of intact marsh (Supplemental Figs. 1 and 2). The chambers are 165 cm high including frusta. Since April 2006 we have maintained two levels of atmospheric CO_2 (ambient and ambient + 340 ppm), throughout the growing season, crossed with two rates of soil N addition (0 and 25 $gm^{-2}y^{-1}$). There are 5 chambers with each combination of CO_2 and N.

Productivity Estimates

A CropCircle active, handheld NDVI sensor (ACS 210, Holland Scientific, Lincoln, NE) was used to measure canopy reflectance roughly every 2 weeks over the course of two growing seasons (2008 and 2009), with periodic measurements in the off-season. To minimize unwanted effects on reflectance measurements (Silva et al. 2008), we avoided measuring during the following situations: flooding events when the water level was more than 5 cm above the soil surface; rain events; periods when the vegetation and litter were moist and when snow or ice were present. Briefly, a modulated polychromatic LED array emits light in two bands, 590 nm and 880 nm over the same footprint. Detectors measure light reflectance in two bands, from 400 to 680 nm and from 800 to 1,000 nm. The light sources cycle on and off rapidly, at 20 Hz and the detectors register reflectance readings at 40 Hz. By subtracting out the "dark" readings between light pulses in a pairwise manner, the sensor generates reflectance measurements that are insensitive to ambient light in the range of natural conditions. We mounted the sensor and peripherals (battery, logger, trigger) on a customized boom equipped with a leveling device that allowed for visual maintenance of a consistent nadir view and height across the chamber (Supplemental Figs. 1 and 2). We attached a fitting onto the boom that temporarily affixed onto the top of each experimental chamber (165 cm high), allowing the instrument to pivot in an arc over each plot while keeping the sensor level. For each chamber measurement, the sensor scanned two swaths (30 cm wide arcs) covering roughly 50% of the ground area (Supplemental Fig. 3). This particular device is engineered so that NDVI is independent of distance from the sensor to a surface in the range from 25 to 210 cm.

We estimated biomass by conventional methods at two points in the growing season using a combination of individual stem counts and allometry for *Schoenoplectus americanus* and biomass clipping for two species of grasses, *Spartina patens*, and *Distichlis spicata* (described fully in Langley et al. 2009a, b). These three species accounted for all the plants in our plots.

Evaluation of Vegetation Indices (VIs)

An ideal VI for estimating plant growth would have a robust relationship with biomass over space, and that relationship would hold through time over various intervals. We compared several indices that have proved effective in wetlands before (Smith et al. 1998; Spanglet et al. 1998), including conventional VIs (DI, NDVI, IPVI and RDVI) as well as more sophisticated ones that minimize the influence of soil reflectance (SAVI0.5 and MSAVI2). To compare the predictive ability of VIs over space, we used multivariate correlation matrices to determine linear correlation coefficients between each index (Table 1) and measured biomass at four points in time. Individual plots were the experimental unit for this analysis. To evaluate the predictive ability of VIs through time, we examined linear correlations between treatment means over the four measurement dates for which we have actual biomass measures. Because one of the measures, MSAVI2, was among the best performing VIs through space and time, we examined it more carefully, comparing its ability to predict CO_2 and N treatment effect sizes in addition to absolute biomass.

Results and Discussion

Performance of VIs

We compared several reflectance VIs (Fig. 1) as predictors of total biomass across a variety of treatments that drastically alter plant productivity, community composition and foliar [N], over 2 years that varied climatically (Fig. 2). While the relationships between the indices and total biomass were generally strong, the relationships with grass biomass were typically more consistent across individual dates (Table 2) because of their lower, more consistent stature, horizontal leaf angle and patterns of senescence. The sedge, *S. americanus*, produces single vertical stems with no horizontal leaf area to reflect light from above. Moreover, having a basal meristem, *S. americanus* browns at the top, which causes poor, and often negative, relationships between the VIs and growth upon the onset of senescence later in the growing season. This problem is magnified slightly by the fact that *Sc. americanus* stands higher than the grasses (typically, 1.5 m compared to 0.5 m) and leaf area that is high in the canopy occupies a larger portion of the reflective field than lower leaf area as seen from a perpendicular perspective.

One of the great advantages of using radiometry in salt marsh plots is that grass biomass is particularly difficult to assess by conventional allometric means, given its numerous stems, low stature and tangled, horizontal growth form. Whereas we can manually count the *S. americanus* stems in each plot and measure each stem height and width in our experiment, no such protocol is feasible for the grasses, *S. patens* and *D. spicata*- stem densities for *S. americanus* range from 300 to 1,200 stems m^{-2}, *S. patens* can yield densities over 10,000 stems m^{-2}. For that reason, we resort to destructive sampling by clipping several small quadrats. In order to

Table 1 The formulae and citations for six vegetation indices (VIs)

Index	Vegetation index	Formula	Reference
DI	Differential	IR-R	(Tucker 1979)
NDVI	Normalized differential	(IR-R)/(IR + R)	(Rouse et al. 1973)
IPVI	Infrared percentage	IR/(IR + R)	(Crippen 1990)
SAVI 0.5	Soil-adjusted	(IR−R)/(IR + R + 0.5)[a](1.5)	(Huete 1988)
MSAVI2	Modified soil-adjusted	(0.5)[a](2[a](IR + 1)−sqrt((2[a]IR + 1)^2−8[a](IR−R)))	(Qi et al. 1994)
RDVI	Renormalized difference	(IR−R)/sqrt(IR + R)	(Roujean and Breon 1995)

[a] IR is the reflectance of radiation in the near-infrared band and R is the reflectance of radiation in the red band

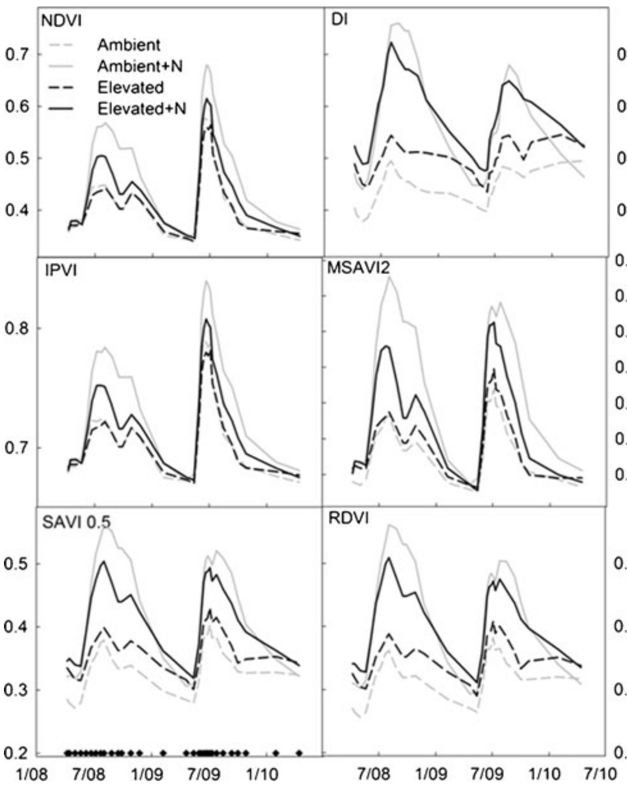

Fig. 1 Six different vegetation indices over 2 years of study, separated by CO_2 and nitrogen treatment groups. Sample dates are indicated by diamonds on the x-axis in the lower left panel

avoid incurring lasting disturbances on plant growth, we clip only a small fraction, totaling 0.45%, of the plot area during each biomass assessment. We conclude that field-based radiometric VIs could provide a valuable alternative method for assessing grass biomass in sensitive experimental plots.

Averaged across dates, all VIs performed similarly (bold numbers, Table 2). Likewise, all VIs predicted grass and total biomass relatively well across dates. Some indices, such as MSAVI2, also exhibited a robust, consistent relationship with total biomass that did not vary strongly over years or different times of year (Table 3, Fig. 3). However, other VIs failed to capture realistic patterns of inter-annual variability; that is, the relationship between the VI and biomass differed through time. For instance, NDVI values for 2008 and 2009 (Fig. 1) suggest that the peak biomass in 2009 was roughly twice that of 2008, while biomass measured by our conventional method was similar over the 2 years (Supplement Table 1). The error may have arisen from differences in amount or reflectance of bare ground between years, which may cause variability in NDVI. Indices like MSAVI2 have a soil adjustment factor in the denominator to separate the plant signal from soil noise (Qi et al. 1994). Such a correction could be particularly important in tidal wetlands that are subject to variability in soil surface properties arising from factors such inundation, sediment or wrack deposition.

Measurements made during the winter or spring before green-up (Figs. 1 and 2) provide a reference condition or zeroing point because there is no green vegetation at that time. During these periods, differences in reflectance are due solely to the characteristics of the senescent plant litter, such as differences in the chemical composition or "quality" of the litter or amount of bare ground. Some indices detected a difference between treatments during the senescent period, or differences between years (Fig. 1), while MSAVI2 indicated that all groups were roughly equivalent over both years, despite the differences in the litter layer. Based on the combination of high correlation coefficients within and among dates for grass and total biomass, and the consistent zeroing among treatments between growing seasons, we concluded that MSAVI2 predicts absolute biomass more effectively than the other VIs examined at our site. We, therefore, conducted more careful analyses focusing on the intra-annual patterns of MSAVI2 and its ability to detect treatment effects.

Intra-annual Patterns of Plant Growth

High-frequency radiometric measurements allow for comparison of intra-annual patterns of plant growth that may not be apparent in conventional biomass assessments at one or two times each year. Interestingly, the Amb + N treatment plots showed higher MSAVI2 in 2008 than 2009, while all other treatment groups yielded the highest values early in 2009, before the conventional biomass assessment in July (Fig. 1). All treatment groups experienced a more rapid green-up and an earlier peak biomass in 2009 than in 2008, possibly due to warmer temperatures in early summer (Fig. 2).

In 2008, drought in Jul and Aug was followed by a relatively wet September, which may have stimulated a late-season pulse of growth and relatively high MSAVI2 values in late October, 2008 (around day 300, Fig. 2). This peak would not have been captured by the biomass assessment, which occurred on October 6, 2008. Examining differences in response among treatments may afford inferences about how elevated CO_2 and N interact with other climatic variables. For instance, the ambient + N group did not exhibit the rise in MSAVI2 during the autumn of 2008 like the other treatment groups (Figs. 1 and 2). The species composition between in the ambient + N group was dominated by the grasses, *S. patens* and *D. spicata* (Supplemental Table 1), which are more salt-tolerant than *S. americanus* (Broome et al. 1995). Perhaps, the increase in precipitation in late 2008 after a relative droughty stretch alleviated salinity-stress and afforded the *S. americanus*-dominated plots a late pulse of growth that was not apparent in the grass-dominated plots.

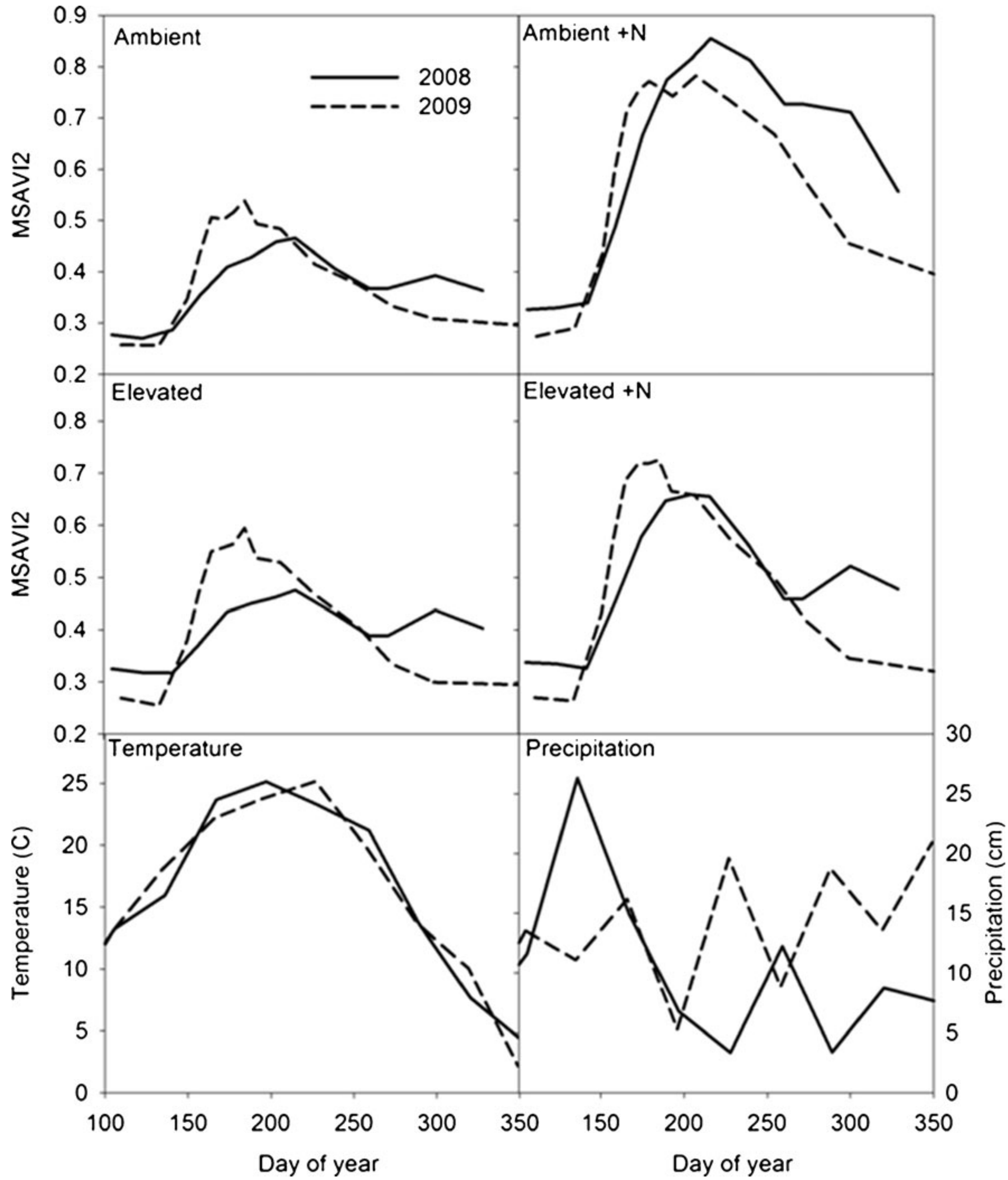

Fig. 2 Patterns of MSAVI2 for each treatment, mean monthly temperature and monthly precipitation over 2 years (2008: *solid lines*; 2009 *dashed lines*)

Radiometric VIs allow for comparison of treatment effects on the length of the growing season. A previous study using NDVI reported that elevated CO_2 may delay autumnal senescence (Taylor et al. 2008). Here, most VIs revealed no strong differences in the course of autumnal senescence according to CO_2 treatment; however, several VIs, including NDVI and MSAVI2, indicate N-fertilized treatments approach the "zero point" more slowly (Fig. 1). Here again, this pattern appears to follow from the treatment effects on species composition (Suppelementary Table 1). The N-fertilized plots are more dominated by grasses, which senesce more slowly in the fall than *S. americanus* (personal observation).

While remotely sensed VIs have proven valuable for estimating absolute plant growth, they may also be a valuable tool for comparing relative effects of global change treatments to natural background variation. VIs diverged widely regarding treatment effect assessment. One pitfall of comparing treatments is that foliar characteristics that

Table 2 Correlation coefficients between several indices calculated from radiometric data and conventional biomass estimates over four dates spanning two growing seasons. Indices were calculated separately for *S. americanus*, the composite of two grass species or the total biomass of each plot (n=20)

	Date	NDVI	DI	IPVI	RI	MSAVI2	SAVI.5	RDVI
Sc. americanus	Jun–08	−0.01	0.27	−0.01	−0.05	0.00	0.13	0.18
	Oct–08	−0.59	−0.50	−0.59	−0.57	−0.57	−0.55	−0.54
	Jun–09	−0.49	0.04	−0.49	−0.55	−0.37	−0.24	−0.16
	Oct–09	−0.68	−0.37	−0.68	−0.67	−0.70	−0.57	−0.52
	All	**−0.44**	**−0.14**	**−0.44**	**−0.46**	**−0.41**	**−0.31**	**−0.26**
Grass	Jun–08	0.89	0.70	0.89	0.89	0.89	0.83	0.79
	Oct–08	0.89	0.81	0.89	0.89	0.89	0.92	0.89
	Jun–09	0.85	0.62	0.85	0.88	0.83	0.80	0.76
	Oct–09	0.70	0.68	0.70	0.70	0.71	0.76	0.75
	All	**0.86**	**0.70**	**0.86**	**0.86**	**0.86**	**0.83**	**0.80**
Total	Jun–08	0.89	0.85	0.89	0.86	0.90	0.91	0.90
	Oct–08	0.89	0.72	0.89	0.89	0.90	0.83	0.80
	Jun–09	0.70	0.79	0.70	0.69	0.75	0.81	0.82
	Oct–09	0.40	0.57	0.40	0.41	0.40	0.54	0.56
	All	**0.72**	**0.73**	**0.72**	**0.71**	**0.74**	**0.77**	**0.77**

vary independently of biomass may also change with treatments. For instance, NDVI is an indicator of canopy greenness, which is tightly correlated with canopy [N]. While elevated CO_2 stimulates biomass growth, it also consistently reduces foliar [N], and can reduce total canopy N content (Erickson et al. 2007). In the present study, the increased biomass with elevated CO_2 was likely negated by the reduced foliar [N], so that NDVI revealed no CO_2-stimulation of biomass (Fig. 1, difference between elev and amb). Because reduced foliar [N] is very consistent across many CO_2 studies, radiometric VIs, and NDVI in particular, are likely to underestimate CO_2 effects on biomass. Interestingly though, some VIs (MSAVI2, SAVI,RDVI) in the present study, were less influenced by foliar [N] and indicated a CO_2 stimulation of plant biomass consistent with that we measured (Fig. 1).

MSAVI2, which proved a robust predictor through time, also effectively captured variability in plant growth resulting from the global change treatments (Fig. 4). Though the slope of the relationship between MSAVI2 and treatment effect did not change, the intercept depended on the time of year (July vs. Oct.), indicating that radiometric assessment of treatment effects on biomass, like absolute biomass estimates, are sensitive to the course of plant senescence.

Table 3 Correlations among the four treatment groups over each of four sampling times (n=16)

	NDVI	DI	IPVI	RI	MSAVI	SAVI	RDVI
Sc am	0.14	−0.09	0.14	0.12	0.06	0.01	−0.01
Grass	0.60	0.73	0.60	0.57	0.71	0.74	0.74
Total	0.78	0.71	0.78	0.74	0.83	0.82	0.80

Limitations

Previous work using handheld radiometry has concluded that VIs relationships are too confounded with different plant species' architectures to be useful in marshes (Spanglet et al. 1998). Clearly, radiometry may not be widely applied to any ecosystem without careful consideration and calibration. In the present study, across all plots, VIs yielded mostly negative relationships with *Sc. americanus*, which was a significant contributor to biomass in all plots (Supplemental Table 1). Yet, the VIs still proved to be effective predictors of total biomass. This seemingly contradictory pattern can be explained by the wide range of biomass responses generated by our treatment application. N-fertilization increased total biomass, mostly by promoting grasses, which sharply increased in biomass to the detriment of the sedge, generating a negative relationship between sedge growth and total growth. Limiting our analysis to only the unfertilized plots, which had relatively little grass, we see that MSAVI2 does indeed have a positive, though relatively

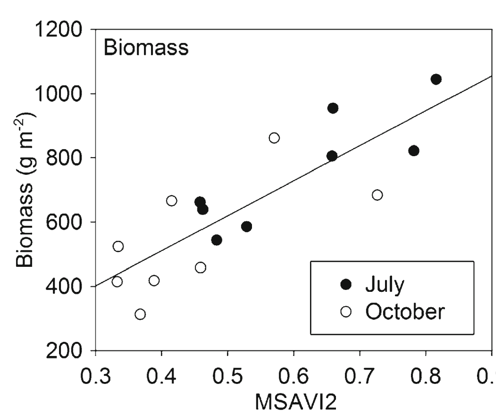

Fig. 3 MSAVI2 versus measured total biomass for each treatment group over each of the four biomass assessment dates

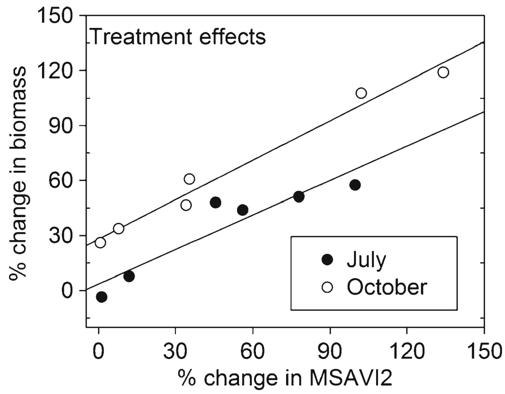

Fig. 4 Treatment effect size on total biomass estimated by MSAVI2 versus that estimated by conventional measurements over 2 years: *solid symbols* represent July sampling dates; *open symbols* represent October. The stimulations relative to control caused by elevated CO_2, N addition and elevated CO_2 + N were calculated as $100\% * (\mathrm{Treatment} - \mathrm{Control})/\mathrm{Control}$

weak, relationship with sedge biomass in July (average correlation coefficient across 2008 and 2009=0.37, n=10). This pattern indicates that the effectiveness of radiometry for assessing biomass is related to the variability among plots- had we not imposed treatments that greatly increased that variability, the correlation with biomass would have been weaker.

Discrepancies between measured biomass and that predicted by VIs could arise from limitations of either measurement. Remotely sensed VIs were originally developed for estimating instantaneous productivity because they relate to leaf area and leaf greenness, both of which should relate positively to ecosystem productivity. Here we relate these reflectance indices to biomass instead of productivity. We have historically used peak biomass, measured in late July, as a proxy for productivity (Arp et al. 1993). Though biomass and productivity certainly covary, peak biomass likely underestimates productivity. A true annual aboveground productivity would incorporate turnover of plant tissues and would include plant growth after peak biomass (Morris and Haskin 1990). We have estimated stem turnover and found that we tend to underestimate productivity of *Sc. americanus* by an amount that varies from 5% to 30% depending on the particular treatment (White et al., in review). Relating radiometric VIs to true productivity, rather than standing biomass, may yield tighter relationships than those presented here.

The use of radiometry in tidal wetlands is potentially hindered by the extremely variable environment that could cause artifacts in the readings. Variability in water level or surface soil moisture could alter reflectance on the ground surface and would affect treatments differently, because the treatment groups vary substantially in the amount of bare ground visible from above. Moisture on leaves and litter, from dew, recent rain, or tidal inundation, can alter reflectance patterns. However, given the ease of use, frequent measurements can be made to mitigate such concerns. Moreover, as in the present study, selection of a VI that that yields consistent readings in the non-growing season can help overcome such confounding effects.

Conclusions

Active radiometric measurements provide a rapid, relatively inexpensive and non-subjective method to assess plant growth that is insensitive to changes in light environment. However, field-based radiometry has proven only moderately effective in wetlands because of irregular canopy characteristics (height, roughness) the confounding effects of species diversity such as variability in foliar spectral qualities (Spanglet et al. 1998). Many wetlands however, have low, even canopies with naturally low plant diversity. We found that in a brackish marsh exposed to atmospheric CO_2 and N manipulations, radiometric indices related well to total plant biomass. Indices that account for variability in soil surface properties, like MSAVI2, were the most robust through time. The VIs assessed here performed particularly well for predicting grass biomass, and quite poorly for sedge biomass. Fortuitously, the properties that make grasses like *S. patens* and *D. spicata* difficult to measure nondestructively also render them well suited to radiometric assessment; they have high densities of fine stems that tend to orient diagonally or horizontally. We feel that field-based radiometric assessment could provide an effective alternative to conventional destructive techniques, particularly in wetland areas dominated by such grasses. Further, the ability to sample quickly and therefore, frequently, can help overcome other sources of variability such as flooding. This approach is less well-suited to areas that have uneven canopy height, those that dominated by species either with tall stature like *Phragmites autstralis* or with vertically oriented leaf area such as sedges and rushes.

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