RESTRUCTURING OF WETLAND COMMUNITIES IN RESPONSE TO A CHANGING CLIMATE AT MULTIPLE SPATIAL AND TAXONOMIC SCALES

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Dissertation

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ABSTRACT

Climate change threatens to alter the current distribution, productivity, and community composition of wetlands in the Midwestern United States. Increasing rainfall variability and rising temperatures will yield unique stresses for wetland vegetation, including an increase in flooding severity and a higher frequency of potentially harmful heat events. This dissertation explores the interactions and impacts of climate warming and hydrologic variability on productivity, morphological plasticity, reproduction, and functional composition within wetland communities, followed by an evaluation of the connection between wetland distribution and climate on a regional scale. Climate warming led to depressions in productivity during the warmest months while hydrologic variation consistent with climate projections yielded decreases in spring production and peak biomass. Reproductive allocation and other functional trait differences suggested that the future climate will limit productivity in many wetland ecosystems in the Midwest. A distribution model based on Artificial Neural Networks projected significant increases in flooding leading to wetland expansion concentrated in the Midwestern Corn Belt and potential declines in wetland area in Minnesota and northern Michigan. These results suggest that, though wetland area is projected to increase for the Midwest, without hydrologic management, many wetland systems are at risk of community turnover and degradation resulting from a shifting climate.

DEDICATION

This work is dedicated to my wife Ashley whose patience and perseverance are immeasurable, our daughter Penelope whose smiles brighten the world, and my parents Berle and Cyndy Garris who believed it was possible.

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CHAPTER I

INTRODUCTION

Why Wetlands?

Wetlands are of particular interest in climate change research because they play a pivotal role in global biogeochemical cycles (Bridgham et al. 2006) and because they are sensitive to minor shifts in temperature and rainfall (Mauquoy et al. 2002; Bridgham et al. 2008). Wetlands are extremely productive ecosystems, exceeded only by tropical rainforests in annual net primary productivity (Keddy 2002). Vegetation decomposes slowly due to the restriction of aerobic catabolism in inundated soils (Neue et al. 1997). This combination of high productivity and low rates of decomposition has yielded high rates of carbon accumulation in wetland soils (Mitsch et al. 2013). As a result, wetlands are often considered to be carbon sinks, and currently store between 2.1 and 10 times more soil carbon per unit area than upland systems (Matthews & Fung 1987; Aselmann & Crutzen 1989; Lehner & Döll 2004; Bridgham et al. 2006). Wetlands can also be sources of atmospheric carbon (Whiting & Chanton 2001). Anoxia, and subsequent anaerobiosis in inundated soils leads to the release of 115-200 Tg of methane (CH_4) from wetlands into the atmosphere each year (Aselmann & Crutzen 1989; Mitsch et al. 2013). Methane is 79-105 times more effective at trapping radiant heat than CO_2 in the short term (Shindell et al. 2009), but eventually degrades in the upper atmosphere into

CO_2 (Smith et al. 2010). All of these processes are mediated by communities of hydrophytes (Gedney et al. 2004; Koelbener et al. 2010), plants that have adapted mechanisms to tolerate frequent inundation (Tiner 1991). Understanding how climate change alters the form and function of these plant communities will be critical for projecting whether wetlands remediate or accelerate future climate change.

Responses may differ between cold and warm regions

Considerable research has addressed the impacts of climate change on wetland communities in cool boreal climates (Chapin et al. 1995; Shaver et al. 2000; Dormann & Woodin 2002; Carlyle et al. 2011) with comparably fewer efforts in warm temperate and tropical regions (e.g Peñuelas et al. 2007; Chimner & Karberg 2008; Gedan & Bertness 2009). Approximately 28% of wetlands are found in the northern hemisphere in cool, moist climates above 60°N latitude (Aselmann & Crutzen 1989) where climate change is anticipated to be the most extreme (Solomon et al. 2008). The few studies that have been conducted in warmer regions suggest that climate change may have different effects on productivity (Peñuelas et al. 2007) and community composition (Gedan & Bertness 2009) than those of cooler climates. It is therefore imperative not only for conservation of wetland biota, but for projecting future feedbacks to global climate to understand the mechanisms governing community responses to climate change in warm temperate regions.

Vegetation at temperate latitudes is anticipated to follow some but not all trends established in the arctic (Chapin et al. 1995; Shaver et al. 2000; Dormann &

Woodin 2002; Carlyle et al. 2011). Warming may augment total productivity by increasing the length of the growing season (Walther et al. 2002), consistent with findings in cooler climates (Hollister et al. 2005; Peñuelas et al. 2007). Warming-induced increases in transpiration have even been proposed to ameliorate water-logging stress at a range of water table depths (Gedan & Bertness 2009). An intensification of episodic heat events can induce mid-season senescence directly in the form of thermal stress and indirectly by increasing the intensity of droughts (Saleska et al. 1999). Cool, well-drained terrestrial systems yield, on average, a 19% increase in production associated with climate warming (Luo 2007) that is a function of growing season extension and increases in N-mineralization rates (Chapin III et al. 1995; Rustad et al. 2001; Dessureault-Rompré et al. 2010). Plant communities occurring in warmer climates may only infrequently exploit these advantages, as growing season extensions will be punctuated with severe flooding and stressful heat events. As a result, mid-latitude emergent marshes will likely exhibit a higher rate of stress and disturbance relative to historic conditions.

Quantifying the stress-disturbance gradient: beyond standing crop

The timing and quantity of primary production is a critical component of the community response to changing conditions. Theory suggests that climate warming will act on communities by altering pre-existing stress-subsidy gradients (Odum et al. 1979) and the rate of disturbance (Grime 1993)(here termed the stress-disturbance regime). Stress reflects shifts in abiotic factors that place limits on productivity by reducing the rate of tissue formation (Grime 1979), while subsidies are factors that augment production (Odum et al. 1979). Disturbance also places limits on production, but by removing or irreparably damaging plant tissues (Keddy 2002). Under this framework, the plant community has a unimodal response to changes in conditions (sensu Odum et al. 1979). Near maximum productivity, declines in productivity would be termed stressful, while shifts towards extreme conditions would increase the frequency of disturbance.

Climate warming and shifting hydrologic regimes in the future will likely lead to differences in peak biomass (i.e. standing crop); the maximal amount of living material observed within an annual cycle). In forested systems, this may mean shifts in turnover that will only be realized over relatively long periods of time (5-100 years). In emergent marshes, where peak biomass is the product of 1-2 seasons of production, these effects may be noticeable within a single growing season. In high-turnover systems, standing crop represents a net accumulation of biomass that masks potential variability in the timing of production and the rate of disturbance. For example, high rates of tissue removal (disturbance) may be compensated for by augmented total production, yielding little difference in peak biomass, but marked differences in community characteristics. Furthermore, stressful conditions in the early and mid season may be compensated for by subsidies in the late season when falling temperatures begin to limit production.
It is therefore necessary to understand how climate change will impact variation in productivity at multiple time-points during the growing season to understand the changing selective pressures placed on wetland communities in the future. Warming

and increasing hydrologic variability anticipated in the coming century may yield markedly different rates of production at different points within the growing season.

Non-destructive approximations of productivity have been developed by geographers to document shifts in vegetation patterns at large spatial scales (Pearson & Miller 1972; Tucker 1977; Tucker 1979; Tucker et al. 1985; Huete 1988; Jackson & Huete 1991). Remote-sensing can be used to generate proxies of instantaneous production (the rate of photosynthate formation per unit area) using spectral reflectance properties unique to the photosynthetic process (Tucker et al. 1985; Christensen & Goudriaan 1993). Here I use plot-level remote sensing to characterize differences in productivity at multiple time-points throughout the growing season. These shifts in productivity can be translated to changes in the stress-disturbance regimes experienced by wetland communities subjected to future climate conditions.

Quantifying the community response: a trait-based approach

Countless attempts have been made to summarize the complexity inherent in vegetation in ways that reliably connect plant communities to the abiotic conditions in which they form (e.g.(Raunkiaer 1934; Grime 1979; Tilman 1988; Craine 2009; Shipley 2010). Grime proposed one such theory (CSR Theory) by grouping vegetation into three categories based on trait similarities found along gradients of stress and disturbance (Grime 1977; Grime 1979; Grime 2001). Species that proliferate under benign conditions (C) (low-stress and low-disturbance) were thought to exhibit traits associated with competitive ability (increased canopy height, seed mass, and specific leaf area

(SLA)(Westoby 1998)). Species that performed well in stressful environments (S) expressed traits associated with the preservation of vegetative tissues (increased leaf longevity, decreased stature and SLA). Finally, species in frequently disturbed environments (R) expressed traits associated with regeneration (short-lived, low seed mass, high seed number). Changes in conditions can affect the relative amounts of stress and disturbance experienced by vegetation. It is therefore possible to use trait variation as evidence of shifting stress-disturbance regimes in addition to components of productivity. This model, and subsequent derivations, have been successfully applied at the local and regional scale under a variety of environmental contexts (Swenson & Weiser 2010; Schmidtlein et al. 2012). In this study I pair within-season measures of productivity with community-weighted traits to diagnose shifts in the stress-disturbance regime experienced by individuals and the community.

Goals

This dissertation evaluates the potential impacts of climate change at multiple spatial, temporal, and bio-organizational scales in efforts to produce a more comprehensive understanding of how temperature and hydrology shifts consistent with climate projections will alter existing wetland communities within the Midwestern United States. In Chapter 2, I test the specific effects of temperature elevation in the field via Open Top Chambers (OTCs) on the timing and magnitude of productivity integrated throughout the growing season and on community composition and functional structure in a natural wet meadow community. In chapter 3, I perform a similar field manipulation of temperature, except in a near monoculture of *Leersia oryzoides* stratified along a semi-natural hydrologic gradient to assess the effects of climate warming on productivity and reproductive mode of this morphologically plastic grass. In chapter 4, I test the impact of hydrologic variability expected in the coming century on communities established in artificial mesocosms. In chapter 5, I develop predictive models of wetland composition and distribution for the Midwestern US that are derived from regional climate forecasts and a host of geographically distributed factors thought to be associated with wetland prevalence on a landscape scale.

CHAPTER II

CLIMATE WARMING AT TEMPERATE LATITUDES : EFFECTS ON PRODUCTIVITY AND COMMUNITY-AGGREGATED FUNCTIONAL TRAITS

Abstract

I evaluated how climate warming affects productivity and functional trait composition in a temperate wet meadow. Warming via open top chambers elicited a 4-fold increase in the frequency of potentially damaging heat events during June and July 2010, with some exceeding 8°C above ambient. Chambers were ineffective the second year, which was punctuated by record rainfall and associated cloud-cover. Proxy measures of chlorophyll content and functional mesophyll suggested that heat episodes were stressful, decreasing mid-season production relative to control plots. There were significant negative relationships between total degree days and community-weighted mean plant height and between total degree days and community-weighted seed mass. These results suggest that an increasing frequency of episodic heat events brought about by climate change will increase the disturbance frequency in non-arid, mid-latitude habitats, leading to a decreased prevalence of disturbance-intolerant species.

Introduction

Climate warming may alter the future productivity and vegetation structure of wetlands in the Midwestern United States. Analogous periods of climate warming in the past have led to long-lasting shifts in vegetation. Cole et al. (2010) examined periods of rapid warming in the late Holocene, which saw vegetation shifts towards early-successional communities that persisted for 4000 years. Climate change has already yielded systematic shifts in natural communities (Parmesan & Yohe 2003) in terms of phenology and composition and many studies have attempted to predict how current communities will change in the near future.

Numerous experiments have been conducted to test how climate warming will affect natural communities, and have documented significant impacts of warming on plant-mediated nutrient and carbon cycling (Aerts et al. 2009), phenology (Hollister et al. 2005), the duration of the growing season (Walther et al. 2002), productivity (Luo 2007), species diversity (Gedan & Bertness 2009), trophic dynamics and reproductive output (Liu et al. 2011), and morphology (Hollister & Webber 2000; Fraser et al. 2009). Despite this seemingly comprehensive understanding of climate-warming effects, some critical gaps remain. An overwhelming majority of these warming experiments were conducted in cool sub-arctic climates (Chapin III et al. 1995; Shaver et al. 2000; Dormann & Woodin 2002; Carlyle et al. 2011) or in cool mountainous regions (Suzuki & Kudo 1997). Cool climates have been the traditional focus of field experiments because they are projected to exhibit the most rapid warming (Henry & Molau 1997; Solomon et al. 2008) and because the vegetation of warmer climates was generally thought to be more resilient to temperature shifts than tundra and sub-arctic vegetation (Peñuelas et al. 2007). The few studies that have been conducted in warmer climates suggest that some, but not all, responses are similar to those documented in cooler climates. Farnsworth et al. (1995) demonstrated that forbs were more responsive to soil warming than woody species in the Duke Forest, consistent with findings in cooler climates (Luo 2007). Peñuelas et al. (2007) found that warming tended to increase production in cooler, northern sites (M=50°N Latitude) consistent with countless findings in the literature (see Rustad et al. (2001) for a meta-analysis), but warming decreased production at a site with the warmest climate (41°N Latitude). Finally, Gedan and Bertness (2009) documented more rapid community turnover in southern sites than northern ones in response to artificial warming of native forb panne vegetation (also at ~41°N Latitude). These results suggest that some communities may be less resilient to climate warming at temperate latitudes than previously thought (Peñuelas et al. 2007).

Theory suggests that climate warming will act on communities by altering pre-existing gradients of stress and disturbance (Grime 1993). Stress reflects combinations of abiotic factors that place limits on productivity by affecting the rate of tissue formation (Grime 1979). Disturbance also places limits on productivity, but by removing or irreparably damaging plant tissues (Keddy 2002). Therefore, productivity represents a major response to the stress-disturbance regime, where higher yields are indicative of decreases in stress or disturbance (Grime 1979). In this study I evaluated the impacts of climate warming on productivity and functional composition in wetland communities to answer two questions (1) How does warming affect productivity in temperate wetlands?

and (2) What are the implications of changing productivity on the functional structure of wetland vegetation?

How does warming affect productivity in temperate climates?

The following model indicates how I hypothesize productivity, integrated over time, will respond to climate warming at temperate latitudes (Figure 2.1). Similar to cool climates, I predict climate warming to lead to an earlier onset of production in the spring, and a later onset of senescence in the fall.

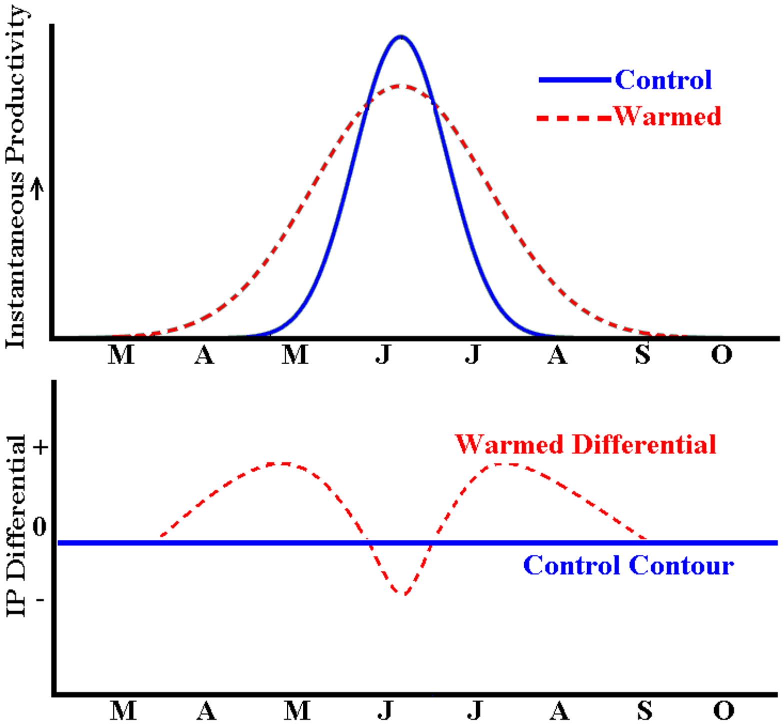


Figure 2.1. A graphical model predicting shifts in productivity resulting from climate warming at temperate latitudes. The model (above) describes the rate of new tissue formation throughout a typical growing season at temperate latitudes (~40°N) for current (solid line) and future (broken line) temperatures. The differential (below) represents the expected differences in production between plots subjected to warming and controls.

However, at temperate latitudes, heat stress events may be an important factor in determining total productivity. The midwest is characterized by considerable temperature variability, and heat events (temperatures above thresholds known to induce leaf tissue damage) are projected to increase in duration and severity during the warmest portions of the growing season (June-July). As the model addresses seasonal variation in productivity rather than strictly net primary production, I assessed the effects of experimental warming on repeated, non-destructive proxy-measures of productivity throughout two growing seasons.

What are the implications of changing productivity on functional vegetation structure?

Recent evidence suggests that functional trait means aggregated at the level of the community are strongly associated with discrete climate regimes (Swenson & Weiser 2010). These traits reflect functional vegetation structure in that they represent shared trade-offs in life-history and morphology that are related to the past degree of stress or rate of disturbance experienced by communities (Shipley 2010). Here I use traits comprising Westoby's Leaf-Height-Seed Scheme (Westoby 1998), to evaluate community responses to climate warming in terms of stress and disturbance (Grime 1979;2001). Westoby proposed, consistent with Grime's CSR theory (Grime 1977;1979), that specific leaf area, mature plant height, and seed mass were sufficient to resolve species associations along gradients of stress (reduced productivity) and disturbance (rate of tissue damage/removal). Specific Leaf Area (SLA) is strongly associated with resource allocation to leaves that increases with relative growth rate (Poorter & Garnier

1999; Shipley 2010), and decreases with leaf longevity (Reich et al. 1992). Plants with low SLA values tend to occur in stressful environments where scarce resources select against rapid growth and favor slow tissue turnover (Grime 1979; Grime 2001). Plant height and seed mass reflect tradeoffs related to competitive ability along a gradient of disturbance frequency (Westoby 1998). Low rates of disturbance favor species that are tall and produce large seed to compensate for the lack of photosynthetically active radiation near the soil surface (Grime 1979; Grime 2001). I hypothesized that shifts in the timing and amount of productivity reflected by Figure 2.1 would lead to two axes of variation in community aggregated traits. First, the extension of the growing season would lead to traits associated with an increase in total productivity (i.e. increasing specific leaf area). Second, increasing heat stress would yield traits associated with increasing disturbance (i.e. decreasing height and seed mass).

Study Area

This study was conducted over two growing seasons (April-November 2010 & 2012) within a remnant wet meadow – emergent marsh complex on the Bath Nature Preserve (Summit County, Ohio, USA). The remnant wetland was historically drained via tiling and diversion of stream overflows for agriculture. Historic drainage tiles, though present, were no longer effective at the experiment onset, evidenced by the presence of exposed, broken clay tile throughout the site, frequent and persistent flooding in spring, and the proliferation of hydrophytes. The experiment was conducted within a 30mX30m grid that was situated within a mixture of grasses (predominantly *Agrostis* *stolonifera* and *Poa pratensis*), other graminoids (*Carex vulpinoidea*, *Juncus effusus*, and *Scirpus cyperinus*) and forbs (predominantly *Verbena hastata*, *Dipsacus fullonum*, and *Cirsium arvense*).

Materials & Methods

Experimental warming began on June 7th, 2010 using Open Top Chambers (Marion et al. 1997). Open Top Chambers (OTCs) were constructed using 5cm x 5cm x 100cm wooden stakes, driven in a 1.5m x 1.5m square, angled inwards for a 70° dihedral angle, then wrapped in Tufflite IV® greenhouse plastic (Berry Plastics Corp. Evansville, IN) to enclose the sides of a volume of $1.12m^3$ with a $1m^2$ opening at the top. Chambers were of similar construction to those used by Carlyle et al. (2011) except 10cm taller to accommodate taller vegetation. Similar structures have proven effective at mimicking climate change in the form of a 1-6°C elevation in temperature at northern latitudes (Hollister & Webber 2000), and have recently been used successfully in mid-latitude marshes (Gedan & Bertness 2009). A structural control treatment was included to account for potential artifacts imparted by the chamber including reorganization of within-plot trophic structure (Moise & Henry 2010), the provision of drip-lines, differential shading, and a climbing substrate for vines and decumbent species. Un-manipulated controls were designated with survey flags while structural controls comprised wooden stakes wrapped with deer netting (1.5cm x 1.5cm mesh) to mimic the boundaries of the plastic structure. Plots were distributed in a randomized latin square arrangement (n=6 plots of each treatment) to stratify across potential spatial gradients in hydrology and soil chemistry (Cochran & Cox 1957). As recommended by Marion et al. (1997), greenhouse plastic and mesh were removed upon the first major snowfall in November of 2010, and re-established in March of 2011 as chambers tend to act as snow breaks (Bokhorst et al. 2013).

Temperature

A random subset of plots (n=4 per treatment) were instrumented with dataloggers (Thermochron iButton model DS1921G-F5, Embedded Data Systems Inc.) at 12cm above the soil surface that recorded temperature at 30 minute intervals throughout the growing season and into the fall. The samples used for analysis include 222 observation days for which concurrent records were collected for all instrumented plots (some data-loggers were lost due to moisture intrusion). Dataloggers were retrieved every 2 months and randomly reassigned to plots.

Mean temperature, total degree days (TDD), and heat stress degree days (HSDD) were calculated for three, 13 day periods (June 29th-July 11th, October 15th-27th, and November 12th-24th) with full data coverage in both years. This approach was taken rather than a comparison of the entire record to maximize comparability between 2010 and 2011 datasets (the three chosen periods have overlapping, complete records for the same dates in 2010 and 2011 (Figure 2.2)), to minimize the effects of inter-seasonal variation on treatment comparisons, and to test for treatment temperature departures under different contexts (i.e. regional mean temperature/precipitation patterns, insolation, and plant canopy shading).

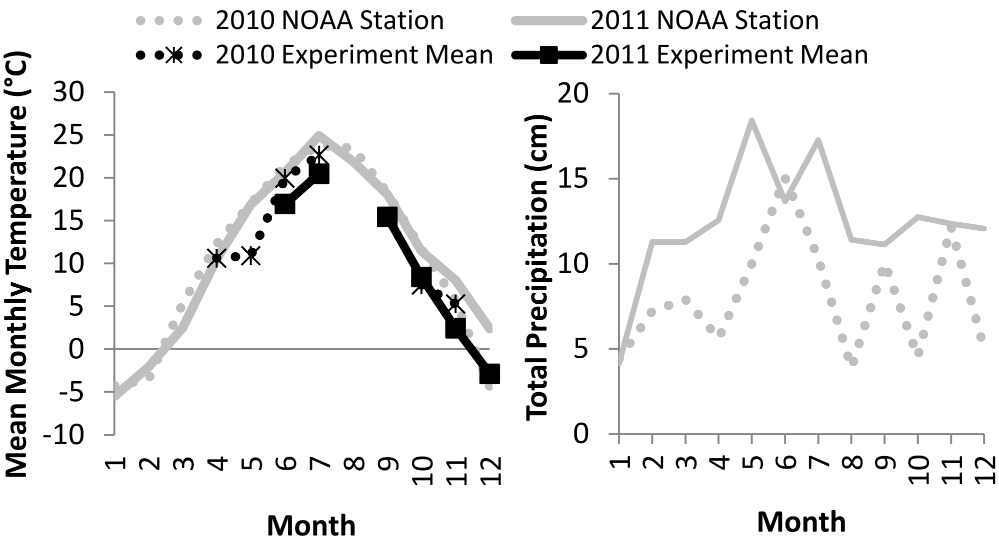


Figure 2.2. Regional Temperature & Precipitation Records. Mean ambient temperatures (black) are displayed alongside temperature records for a NOAA meteorological station (grey) ~34 km SSE of the field site. (Right) Precipitation totals/month are reported for the same meteorological station. Data collected in 2010 are represented by dotted lines, while 2011 data are represented by solid lines.

The Total Degree Day (TDD) is familiar metric in horticulture and other disciplines that is more strongly associated with growth and developmental progress than mean temperature (McMaster & Wilhelm 1997). Though accounting for the impacts of low temperature on growth, the TDD concept ignores any effect of heat stress on productivity (high temperatures are erroneously inferred as being continually more productive). To document heat stress, I used the same degree day calculation, but with a lower temperature threshold thought to be stressful to a wide range of species.

Base temperatures (4.4 & 35°C) were selected as conservative estimates of the onset of production and onset of damage to vegetative tissues for a mixture of cool season grasses and forbs. The lower threshold (4.4°C) is the higher of the two commonly-used base temperatures for plant growth in temperate regions (0°C and 4.4°C respectively (Botkin 1993)) resulting in a more conservative estimate of the integrated period during-which these communities are productive. The higher threshold of 35°C is known to limit photosynthetic output (Crafts-Bradner & Law 2000; Griffin et al. 2004; Barnabás et al. 2008; Barnabás et al. 2008) and is above the reported limits for successful regeneration of many crop species (Wahid et al. 2007) for which temperature reaction norms are well defined. Accumulated total degree days (TDD = $\sum_{4.4°\mathrm{C}}(Tobs - 4.4°\mathrm{C}) * Time$) and accumulated heat stress degree days (HSDD = $\sum_{35°\mathrm{C}}(Tobs - 35°\mathrm{C}) * Time$) were calculated for each of the three 13 day periods (see Morrison & Stewart (2002) for a similar heat accumulation index). Differences among treatments were analyzed via ANOVA using JMP PRO 10 Statistics® (SAS Institute, Cary, NC). Diurnal variation in temperature differences were compared among treatments via repeated measures ANOVA (JMP PRO 10 Statistics®)

Productivity

The ratio vegetation index (RVI) (Pearson & Miller 1972) was calculated for 14 time-points throughout the 2010 and 2011 growing seasons and used to test for treatment effects on the timing of production. RVI is a proxy for the amount of vegetation per unit area (Pearson & Miller 1972) and represents one of the earliest and most frequently used vegetation indices (Jackson & Huete 1991). Although many vegetation indices have been developed since RVI (e.g. NDVI, SAVI, etc…), RVI was chosen for its sensitivity when vegetation density is high (Jackson & Huete 1991). The system studied here was characterized by rapid accumulation of vegetation in the spring and high vegetation density in early June when heat stress events were hypothesized to be most frequent. RVI represents the ratio of near infrared reflectance (760-900nm) over red reflectance (630-690nm), which were measured between March-August using a TetraCam ADC® multispectral digital camera (Tetracam Inc. Chatsworth, CA). Plot photos were taken from a leveled mount 1.4m above the soil surface at the center of each plot (comprising 0.81m^2 or 36% of plot area coverage at the soil surface). Multispectral images were color-processed using TetraCam PixelWrench2® software and individual reflectance values extracted using ImageJ® (Rasband 1997). NIR reflectance is strongly associated with area of functioning mesophyll while far red reflectance is an inverse indicator of foliar chlorophyll content (Broge & Leblanc 2001; Carter & Knapp 2001). The ratio vegetation index (RVI) calculated as the ratio NIR/Red (Pearson & Miller 1972) combines these proxies of foliar area and chlorophyll content (Tucker 1977) into a single estimate of instantaneous production. For a discussion of correlations between vegetation indices and production see Christensen & Goudriaan (Christensen & Goudriaan 1993). Time-weighted mean RVI values were calculated for concurrent periods (differing by no more than 3 days), in June, July, and August of 2010 and 2011. These were analyzed via repeated measured ANOVA (JMP PRO 10 Statistics®) to assess treatment effects.

Community Composition

The relative abundance of each macrophyte species present was estimated visually for each plot by first recording the identity of each species, then ordering these species from greatest to least contribution to aerial coverage, and finally by estimating fractional contribution of each species to total cover (starting with the most abundant species)(see Greig-Smith (1983) for a discussion of visual cover estimation methods). This approach led frequently to estimates of cover >100%, and species cover values were divided by total cover before analysis so that compositional differences reflected relative, rather than absolute cover. Composition estimates were compared only for June and July to minimize inter-seasonal variation in plant cover (Kennedy & Addison 1987) and species-specific responses were only evaluated for species with >30% mean coverage (across all sampling dates) to minimize the effect of observer error. A two-way ANOSIM (Clarke 1993) was conducted to evaluate the effects of treatment and observation date on plot-level community similarity for all recorded time-intervals and followed by appropriate univariate tests. ANOSIM and similarity percentages are described by Clarke (1993) and were conducted using PAST statistical software (Hammer et al. 2001).

Community Structure and Functional Traits

Trait values reported in the literature comprising specific leaf area, maximum (program) height, and seed mass were compiled for each species into a single database. See Appendix A.1 for trait sources. Literature-reported values were considered applicable at the local-scale for these traits, because they are considered to be relatively stable within species over environmental gradients (Garnier et al. 2007). Congeners were used when species-specific estimates were unavailable and grand trait means across species were inserted for all trait values that were not found in the literature for the represented genera (Appendix A.2). Grand means were used instead of treatment-specific means as a more conservative test of treatment-specific effects. The relative abundance matrix was multiplied by trait values and means were generated for each plot at each time-point when abundance was recorded in the field. Abundance-weighted trait means were chosen over un-weighted means (in contrast to Ackerly (Ackerly & Cornwell 2007)) because the comparison here specifically targeted trait variation as a function of shifting abundances, rather than community turnover, and because patterns of trait dispersion are thought to be more stable for abundance-weighted measures than for unweighted ones (Schamp et al. 2008). Differences in plot-level functional trait means were compared between concurrent observation periods in 2010 and 2011 via repeated measures ANOVA.

Results

Open top chambers increased temperature (+3°C) and heat stress (HSDD) between 11AM and 7PM in 2010 ($F_{1,9}$=6.29, p=.034, $F_{1,9}$=8.28, p=.018 respectively), but not in 2011 ($F_{1,9}$=.003, p=.9, $F_{1,9}$=.77, p=.4 respectively) as indicated by independent repeated measures ANOVAs with planned contrasts between OTC and control treatments (Figure 2.3).

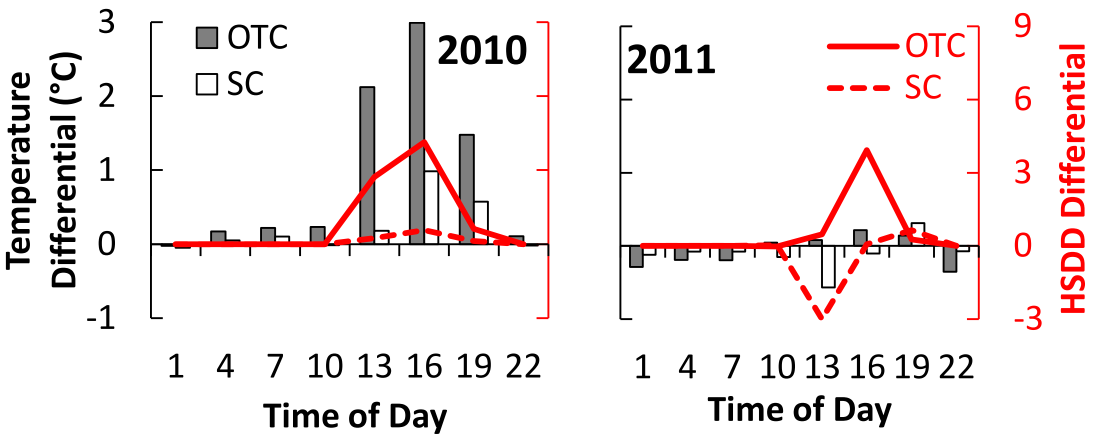


Figure 2.3. Diurnal variation in Mean Temperature (bars) and Heat Stress (HSDD)(lines) for Open top chambers (grey bars/solid lines) and structural controls (white bars/dotted lines). All values are expressed as differences from unmanipulated controls.

Mean temperature differences from controls increased at ambient temperatures greater than 15°C in 2010 but not 2011 (n=4996,3901 respectively)(Figure 2.4).

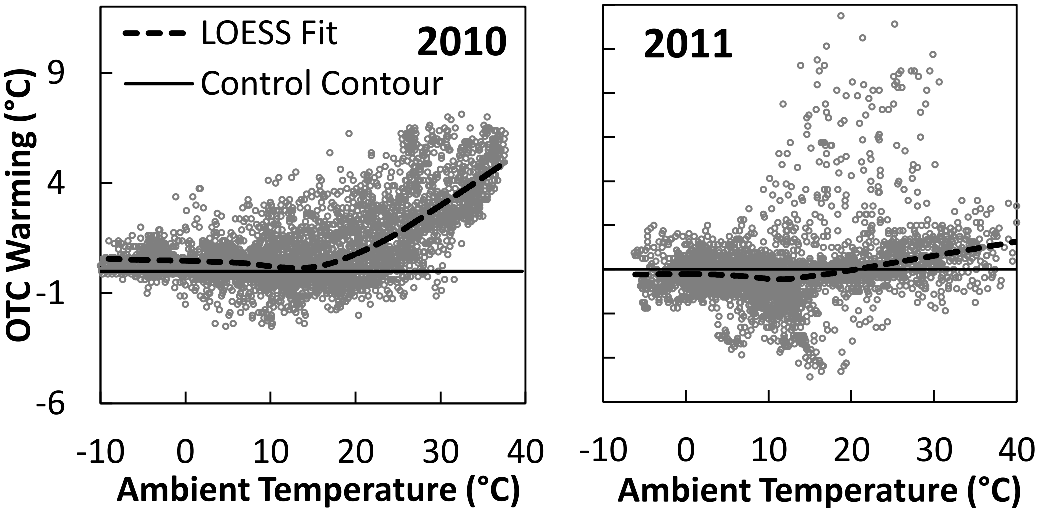


Figure 2.4. Warming effect of OTCs represented as a function of ambient temperature for the year 2010 (left) and 2011 (right). OTC means are represented as differences from control means (n=4). Points above the control contour are warmer than controls (cooler below). Local regression fit lines were generated following the LOESS method (Cleveland 1979) to accommodate the apparent break-point in warming effect at 20°C in 2010.

Open Top Chambers exhibited a 3-4 fold increase in heat stress (HSDD) in July 2010 (Table 2.1), indicating these chambers were subjected to episodic heat stress during this period at a higher rate than the remaining treatments (Cohen's $d=1.77 > 0.8$, indicating a large effect). Open top chambers were warmer than controls except in October and November of 2011, where this reversal (OTCs differed from UCs by -0.6°C) was likely due to differential shading from a declining maximum solar elevation angle in the fall.

The apparent decline in warming effectiveness from 2010 to 2011 is likely the result of record high precipitation totals and concomitant cloud cover in 2011 (NOAA 2010; NOAA 2011), which may have ameliorated treatment effects (Figure 2.5). An analysis of records from a nearby weather station indicated that cloud cover was significantly higher in 2011 than in 2010 (Mann-Whitney $U_{87,116}=4268$, $z=-2.2$,$p=0.028$), and OTC effectiveness declined significantly when cloud cover was >75% ($F_{3,201}=4.395$, $p=0.005$).

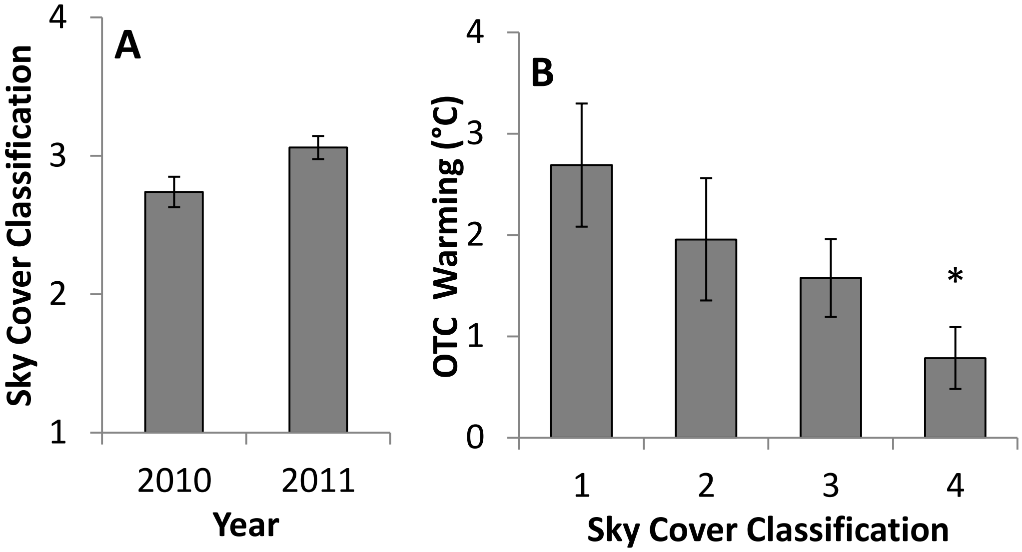


Figure 2.5. Sky cover may explain differences in treatment effect between years. (A) Sky cover was significantly higher in 2011 than 2010. (B) OTC warming effect declines with increasing cloud cover. (*) indicates a significant difference from remaining classes. Sky cover classifications indicate the relative percentage of the visible sky obscured by clouds (1=0-25%, 2=26-50%, 3=51-75%, and 4=76-100%). All error bars represent 2 X SE. Observations included in this analysis were for the period when OTCs are thought to be most effective (1PM-4PM).

Table 2.1. Temperature Metrics for concurrent periods in July, October, and November for similar Julian days in 2010 and 2011. TDD and HSDD refer to accumulated total degree days and accumulated heat stress degree days respectively.

Plot	July		October		November		Grand
Type	2010	2011	2010	2011	2010	2011	Total
			Mean Temp (°C)				
OTC	21.5	21.7	8.2	7.7	4.3	5.4	11.5
SC	20.4	21.3	7.8	8.2	4	5.5	11.2
UC	19.9	21.4	7.8	8.3	4.1	6	11.3

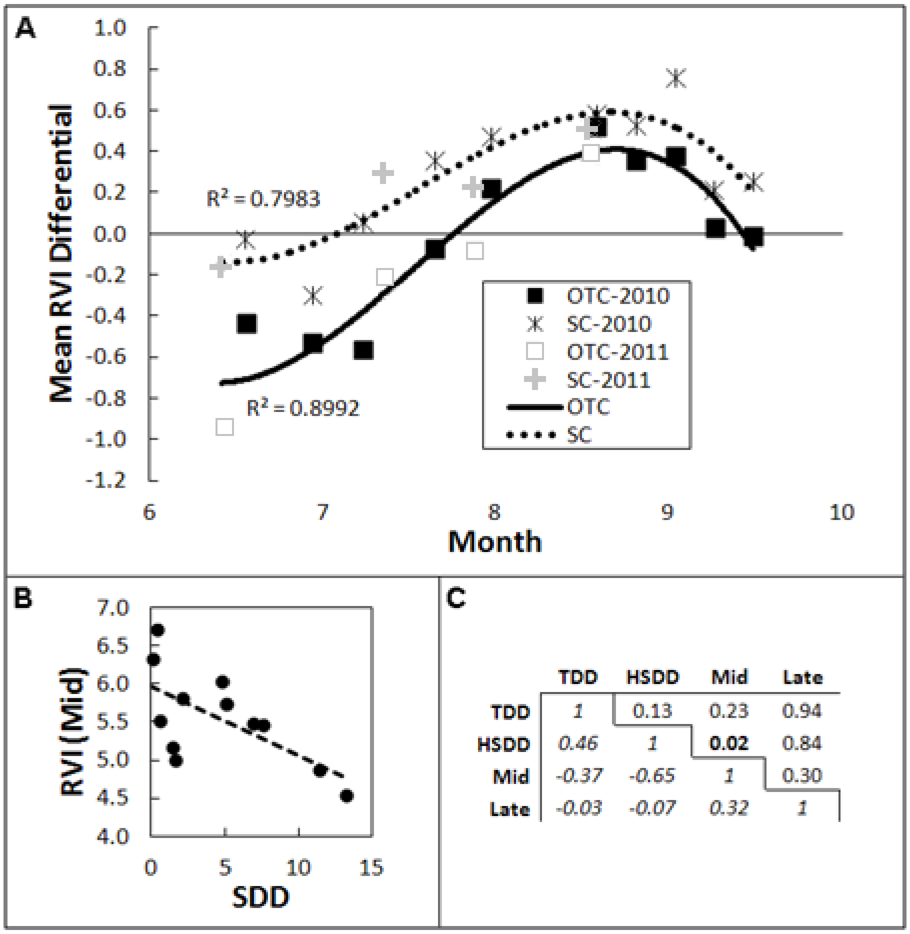
Table 2.1. (cont.) Temperature Metrics for concurrent periods in July, October, and November for similar Julian days in 2010 and 2011. TDD and HSDD refer to accumulated total degree days and accumulated heat stress degree days respectively.

Plot	July		October		November		Grand
Type	2010	2011	2010	2011	2010	2011	Total
			Total Degree Days (TDD)				
OTC	222.2	224.6	73.5	48.5	41.1	33	107.2
SC	208.5	219.8	70.8	54.5	37.2	34.2	104.2
UC	202.2	221.6	70.3	55.5	38.9	39.7	104.7
			Heat Stress Degree Days (HSDD)				
OTC	8.5	5.5	0	0	0	0	2.3
SC	2.9	2.5	0	0	0	0	0.9
UC	2.2	4.5	0	0	0	0	1.1
			Daily Temperature Range				
OTC	41	36.4	35	13.9	36.1	21.9	30.7
SC	37.9	34	35.8	14.9	34.5	21.3	29.7
UC	36.1	36.9	34.5	18	34.9	22.8	30.5

Multispectral Image Analysis

I predicted a relative decrease in productivity for warmed plots in the mid-season (June-July), followed by a relative increase into the Fall (August-September). A repeated measures ANOVA comparing RVI values for all observation dates indicated no significant effect of treatment on RVI response ($F_{2,15}$=0.025,p=0.83).

RVI differentials indicate whether treatments are more or less productive than controls at the time of observation. An examination of these differentials (Figure 2.6 A) indicates that OTCs were less productive than controls in the mid-season, and more productive than controls in the late season. Although non-significant, this is consistent with the model proposed in Figure 2.1. A post-hoc examination of correlations for temperature metrics and productivity indicated that increasing heat stress (HSDD) was associated with decreasing productivity (Figure 2.4 B), while no other relationships existed (Figure 2.6 C).



	TDD	HSDD	Mid	Late
TDD	*1*	0.13	0.23	0.94
HSDD	*0.46*	*1*	**0.02**	0.84
Mid	*-0.37*	*-0.65*	*1*	0.30
Late	*-0.03*	*-0.07*	*0.32*	*1*

Figure 2.6. Ratio Vegetation Index Analysis. (A) Mean RVI differentials from un-manipulated controls (n=6 per treatment) are represented. Trend-lines and associated R^2 values are for 3rd order polynomial functions fit to OTC and SC data-points. (B) Indicates a slight negative association between RVI and HSDD during the mid-season (June-July). (C) Correlation matrix presenting linear r-values (below the diagonal and uncorrected p-values (above the diagonal). No correlations were significant (N=12, adjusted α= 0.05/5, p<0.01).

Community Composition and Structure

Time yielded significant changes in community composition (two-way ANOSIM R=0.077,p=0.048), but treatment differences were not significant (R=0.021, p=0.72) based upon Bray-Curtis dissimilarity coefficients. Subsequent evaluation of similarity percentages indicated that the greatest contributor to plot-level dissimilarity was *Agrostis stolonifera* which was numerically dominant within the field site. Plot level composition did not change appreciably over the study period. Plots just as frequently showed increases in graminoid abundance as decreases, with a maximum increase of 34% and a maximum decrease of 18% for the period between June 2010 and June 2011.

Community Aggregated Functional Traits

Open top chambers induced a significant decline in Specific Leaf Area in 2010 when compared to controls, (F(1,15)=0.392, p=.0284). Univariate tests indicate that this was largely due to a significant decline in late July (F(1,15)=15.245, p=0.0014)(Figure 2.7). Treatments did not differ significantly in terms of height (F(1,15)=0.0112, p=0.92) or seed mass (F(1,15)=0.0064, p=.76).

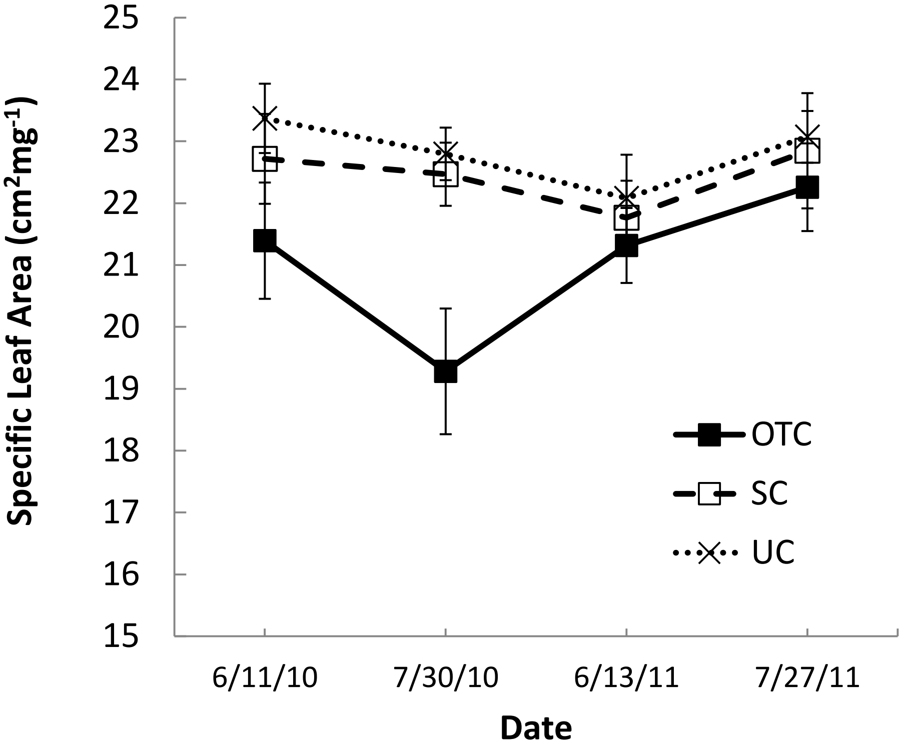


Figure 2.7. Community-Aggregated Specific Leaf Area. Mean specific leaf areas are reported for concurrent observations in 2010 and 2011. Univariate tests indicated that SLA declined significantly for OTCs in July 2010. Treatments did not differ significantly at any other time-point.

Correlations among mean temperature metrics over the entire observation period (with the exception of HSDD for which only July data were included) indicated a strong positive association between mean temperature, accumulated total degree days, and within-period temperature range (Bonferroni-adjusted $p<0.008$)(Table 2.2).

Table 2.2. Temperature metric correlations. Pearson's correlation coefficients are reported below the diagonal with their respective uncorrected p-values above the diagonal. To maintain a type I error rate below 5%, a Bonferroni adjustment indicates that values in bold can be considered significantly correlated (N=12, adjusted α =0.05/6, p<0.008).

	Mean	TDD	HSDD	Range
Mean	1	**0.0000**	0.2386	**0.0023**
TDD	**0.9819**	1	0.1323	**0.0002**
HSDD	0.3684	0.4602	1	0.1160
Range	**0.7887**	**0.8747**	0.4781	1

As a result, only TDD and HSDD were included in a correlation matrix with community-aggregated specific leaf area, mature height, and seed mass (Table 2.3).

Table 2.3. Temperature X trait correlations. Pearson's correlation coefficients are reported below the diagonal with their respective uncorrected p-values above the diagonal. To maintain a type I error rate below 5%, a Bonferroni adjustment indicates that values in bold can be considered significantly correlated (N=12, adjusted α =0.05/10, p<0.005).

	TDD	HSDD	SLA	Height	Seed Mass
TDD	1	0.1323	0.2461	**0.0022**	**0.0034**
HSDD	0.4602	1	0.5191	0.3166	0.0225
SLA	-0.3631	-0.2068	1	0.3467	0.5268
Height	**-0.7913**	-0.3163	0.2981	1	0.0391
Seed Mass	**-0.7699**	-0.6488	0.2031	0.6000	1

Total degree days exhibited significant negative associations with mature height and seed mass (N=12, α adjusted for 10 comparisons, $p<0.005$) (Figure 2.8).

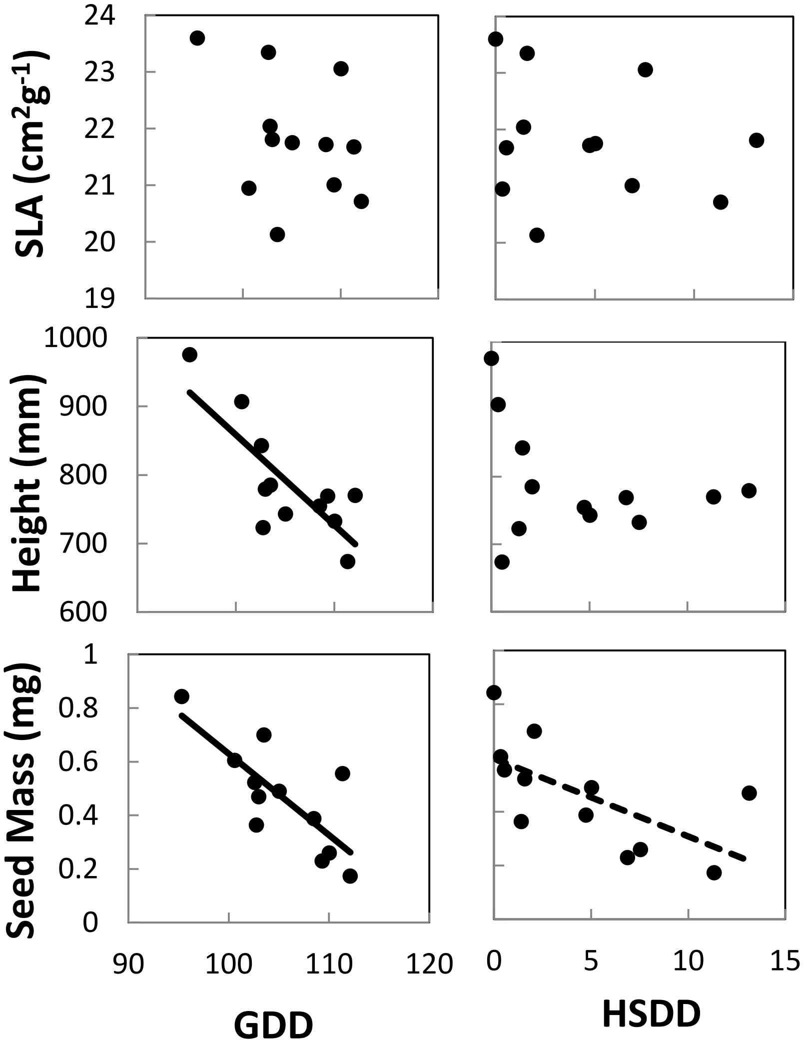


Figure 2.8. Temperature-Trait Relationships. Seed mass, mature height, and SLA (rows) and mean TDD and HSDD (columns) are represented at the plot-level averaged over the entire observation period. Solid trend-lines represent significant linear correlations following a bonferroni-adjustment. Broken trend-lines represent correlations that were significant prior to Bonferroni adjustment (N=12, $p<0.05$).

Discussion

Open top chambers exhibited a 4-fold increase in the integrated duration of heat events (HSDD) in June, 2010 that exceeded the threshold known to impact photosynthesis and reproductive yield (Crafts-Bradner & Law 2000; Griffin et al. 2004; Wahid et al. 2007; Barnabás et al. 2008). Open top chambers differed from controls in mean temperature by a maximum of 1.6°C, consistent with studies performed in colder climates (Marion et al. 1997; Hollister & Webber 2000; Walker et al. 2006; Carlyle et al. 2011). However, the treatment mean difference was not strong (0.1°C for the 222 observation day period), suggesting that OTCs may be better suited to manipulate temperature variability than mean temperature in warmer regions.

OTCs produced the largest warming effect at ambient temperatures above 30°C. This was not consistent with the findings of Carlyle et al. (2011) who determined chambers to be ineffective above 22.2°C in the cooler climate of British Columbia. This suggests that OTC design efficacy may be context-dependent, and treatment effects should not be assumed based on similarity of chamber construction, especially in different climates. The slight cooling in chambers observed in 2011 is consistent with Carlyle's findings at warmer temperatures, suggesting these chambers may not be appropriate for habitats that receive little direct solar radiation (i.e. high cloud cover, rainfall, canopy cover). Hollister and Webber (2005) also documented a decrease in OTC effectiveness in tundra that was associated with greater seasonal precipitation totals.

The apparent lack of correlation between HSDD and other temperature metrics is surprising. One might expect HSDD to be positively correlated with mean temperature or temperature range, as they would increase the likelihood of temperatures exceeding the 35°C threshold (especially considering a strong positive correlation between mean and range). However, HSDD appears to stand alone without any significant association with other temperature metrics, and OTCs are likely the culprit, inducing short episodes of high heat independent of other temperature metrics.

At the individual plot level, chamber effects were idiosyncratic. The plots with the highest and lowest mean temperatures for the entire 222 observation day period were both Open Top Chambers (mean differential of 2°C). This is likely the result of microhabitat variability imparted by differences in vegetation structure. The two plots with the lowest mean temperatures (one an OTC, the other an un-manipulated control) occurred within or on the border of colonizing stands of *Phalaris arundinacea*. These stands were taller and denser than the typical vegetation found around the remainder of the plots and likely resulted in increased shading of dataloggers.

Total estimated production did not differ significantly among plots. This is not surprising, given the observed differences in mean temperature were considerably lower than those reported by other studies (Rustad et al. 2001). Treatment RVI residuals from controls followed sigmoidal relationships (Figure 2.4A). This is consistent with the model of instantaneous production proposed in Figure 2.1. Losses in production (indicated by lower RVI values than controls) were compensated for in the late season (above the control contour) for OTCs, where SCs only showed an increase in production in the late season. The consistency between OTCs and SCs in the late season suggests that this increase in RVI is a non-thermal artifact. However, the decrease in RVI in the early season is a property that is unique to OTCs, and likely linked to HSDD (Table 2.1). The negative relationship between HSDD and RVI further suggests that heat stress events were responsible for this decrease in production (Figure 2.6, B & C).

There were no detectable differences in community composition or functional structure among treatments. This may in part result from a lack of site-specificity in our trait mean calculations. Other approaches employing literature-reported trait means have seen considerable success (e.g. Díaz et al. 1998; Craine et al. 2001) in part from the rapid proliferation of comprehensive (though see Grime (2006)) and accessible trait databases (Bernhardt-Römermann et al. 2008). A recent study by Kazakou et al. (2013) suggests that, though arguably less precise than field measurements (Baraloto et al. 2010), differences between species are sufficiently large for literature-reported trait means to approximate real trait variation at the community level. This lends support for our approach, but does suggest that if treatment responses were slight, trait approximation rather than direct measurement may have yielded differences insignificant.

Community-aggregated plant height and seed mass were both negatively associated with accumulated total degree days even though they did not vary significantly among treatments. One would expect tall, dense stands of vegetation to reduce incident radiation near the soil surface. The observed negative relationship between TDD and height is consistent with this assertion (Figure 2.8). This evidence lends validity to the use of literature-reported functional traits for assessing community responses to environmental variation. However, a similar explanation for observed decreases in seed mass with temperature does not hold. Trait values for the community database were not correlated (maximum linear $r^2 = 0.028$), eliminating the possibility that seed mass could simply be a function of plant height within this community. Rather, these plots are expressing trait convergence in response to micro-habitat variation in temperature and/or other associated environmental factors. Trait convergence is often identified on a local scale in response to gradients of disturbance (Grime 2006), and the strength of the observed relationships suggest that, for these plots, elevated temperatures lead to decreasing seed mass, a plant trait associated with species specialized to more disturbed habitats.

Contrary to our hypothesis, specific leaf area declined significantly in OTCs relative to controls during June, 2010, immediately following the period when OTCs saw an increase in episodic heat events (Figure 2.7). This is not surprising given that open top chambers worked primarily to affect the frequency of heat stress events, rather than uniformly increasing temperature, and chambers were not established until well after the last frost date in 2010. The transience of this effect suggests that heat stress events may have differentially impacted productivity in species with high versus low SLAs where species with higher SLAs saw greater decreases in production than those with low SLAs during the warmest months.

An increase in the rate and extent of tissue damage brought on by episodic heat events may forestall progression to later seral stages, or upset apparent successional equilibria (Johnson & Miyanishi 2007), causing a decline in the prevalence of disturbance-intolerant species. The results reported here, and those of Cole et al.

(2010), support the idea that late-succession species might suffer disproportionately under a warmer, more variable climate, as they are typically less tolerant to tissue damage (Grime 1977). Furthermore, heat events may disproportionately affect the upper canopy (Niinemets & Valladares 2004), leading to leaf senescence and an increase in the level of photosynthetically active radiation reaching the soil surface. These gaps may facilitate the establishment of arriving propagules, accelerating community turnover and decreasing community resistance to invasion (Davis et al. 2000).

The results of this study indicate that episodic heat events consistent with climate projections may increase disturbance frequency during the warmest months at temperate latitudes. Variations in community-aggregated functional traits indicate that these events lead to transient increases in the frequency of disturbance-tolerant species consistent with the findings of Cole et al. (2010). Future studies should evaluate the extent of species-level variation in functional traits in response to climate warming in combination with other climate factors anticipated to shift in the coming century (especially hydrology). Even though literature reported values were shown to be consistent with current theory, population-level variation in trait means and plasticity may lead to unpredictable species-level responses in the long term.

CHAPTER III

EFFECTS OF CLIMATE CHANGE-INDUCED SHIFTS IN TEMPERATURE AND HYDROLOGY ON PRODUCTIVITY AND REPRODUCTIVE STRATEGY OF *LEERSIA ORYZOIDES*

Abstract

Shifts in temperature and hydrology brought about by climate change will likely affect productivity and reproductive output of wetland species. I evaluated the impacts of climate warming via open top chambers in a near monoculture of *Leersia oryzoides* (Rice Cutgrass) distributed along a natural hydrosere. Open top chambers yielded differences in temperature that were small relative to natural variations in temperature found along the hydrosere. An elevated water table and the presence of open top chambers yielded independent stresses relative to ambient conditions. Open top chambers accumulated a greater amount of thatch and produced periodic depressions in productivity, but yielded no significant impacts on total accumulated biomass or reproductive strategy. Areas with an elevated water table were less productive in terms of accumulated biomass, with shorter ramets and a shift from producing predominantly outcrossed to predominantly selfed seeds. Declining productivity and shifts in reproductive mode associated with shifting hydrology may have far-reaching impacts for population structure and gene flow under a changing climate.

Introduction

Climate change has the potential to stress wetland vegetation, reducing productivity and altering reproductive timing and output. Studies to date have shown that warming augments productivity in grasslands (Luo 2007), suggesting that climate warming alleviates stress—where stress is defined as suboptimal productivity resulting from less than ideal environmental conditions (Grime 1979). However, climate warming can have negative effects on reproduction, either by altering seed set and quality directly via thermal stress (Zinn et al. 2010) or by disconnecting plant-pollinator associations (Memmott et al. 2007; Hegland et al. 2009). While many studies have demonstrated that heat events are more damaging under drought conditions than under ample water supply (Barber et al. 2000; Keleş & Öncel 2002; Rizhsky et al. 2002; Griffin et al. 2004; Peñuelas et al. 2007; Barnabás et al. 2008), far fewer studies have addressed a combination of thermal loading and water-logging stress (Bridgham et al. 1999; Weltzin et al. 2000; Chivers et al. 2009), a defining condition for future wetland communities (Spence 1982; Keddy 2002; Mitsch et al. 2009).

Climate forecasts for 2100 project increases in both mean and extreme temperatures and an increase in winter precipitation for the Midwestern United States (USGCRP 2009). Increasing temperature will likely increase productivity in the Midwest, but this will be interrupted by damaging heat events during the warmest summer months (Chapter 2). Climate forecasts for the Midwest include an increase in mean maximum temperatures from 29°C to 34°C by the year 2100 (Hijmans et al. 2005)(Appendix D.1). This increase approaches the 35°C threshold used by crop scientists to predict the onset of heat stress for photosynthesis and reproduction (Crafts-Bradner & Law 2000; Wahid et al. 2007). Climate forecasts also indicate that winter precipitation will increase 17% (Hijmans et al. 2005)(Chapter 5, Appendix D.1) by the year 2100, and decline by 6% in the summer, yielding an augmented spring hydroperiod followed by periods of combined heat and water stress. Increasing winter precipitation will yield, over the long term, an increase in the severity and duration of spring flooding associated with snowmelt. Given these forecasts, I hypothesize that shifts in temperature and hydrology will lead to decreases in productivity in Midwestern wetlands, which will be most pronounced during the spring hydroperiod (as a function of increased flood depth/duration) and during the warmest summer months (June-July) as a result of an increased incidence in heat stress events.

Wetland plants are characterized by their adaptations to survive under varying degrees of water-logging stress (Menges & Waller 1983; Blom & Voesenek 1996; Blom & Voesenek 1996; Jackson & Colmer 2005; Luo et al. 2008). Regeneration can be a major challenge for these species, where germination and recruitment are restricted by oxygen depletion resulting from flooding (Edwards 1933; Keddy & Ellis 1985; Keddy & Reznicek 1986; Jensen 2004) and many species have adapted to regenerate during periods between floods (Blom & Voesenek 1996). Wetland habitats are often subject to floods that remove or bury patches of vegetation, requiring re-establishment via rapid vegetative expansion, or establishment via seed.

Many species within the Poaceae exhibit facultative cleistogamy (Cheplick 2007; Culley & Klooster 2007) in addition to vegetative expansion via rhizomes. In this reproductive system ramets produce adjustable proportions of two types of flowers – cleistogamous (CL) flowers that do not open, and so will automatically self-fertilize, and chasmogamous (CH) flowers which open fully and are capable of outcrossing (Schemske 1978). Theory suggests that allocation to cleistogamous seed in facultatively cleistogamous species depends on stress, where selfed propagules are less energetically costly to produce (in part because they contain relatively few pollen grains per floret (Darwin 1877)) and can provide a means for propagation under suboptimal conditions (Cheplick 2007). If climate change does in fact act as a stressor to native vegetation, theory suggests that this will cause a shift in allocation to cleistogamous reproduction. This may reduce heterozygosity and gene flow among overwhelmingly clonal populations (Knight & Waller 1987; Culley & Klooster 2007). This reduced genetic diversity may limit the capabilities of clonal populations to deal with stresses in the future (e.g. competition with novel invaders or damage from synthetic compounds) or adapt to changing conditions while tracking suitable climates.

I conducted a field experiment to evaluate the combined impact of warming and hydrologic variation on productivity and reproductive mode/output of a dimorphically cleistogamous grass (*Leersia oryzoides*)(Lord 1981; Culley & Klooster 2007). Warming treatments were established via Open Top Chambers (OTCs) and a semi-natural hydrosere reflected variations in hydrology anticipated in the coming century. I hypothesized that depth of spring flooding would yield the most stressful conditions in terms of accumulated biomass, but augmented heat stress via OTCs would have more damaging effects in shallow plots leading to decreases in productivity and the ratio of chasmogamous to cleistogamous flowers. Productivity is often approximated by peak biomass, a variable that does not account for differences in the timing of resource acquisition and growth within populations. Climate warming is predicted to affect both the timing of production and peak biomass. To account for this distinction, I used hyperspectral remote sensing to estimate the potential amount of photosynthate generated at the plot level at multiple time-periods in addition to harvesting biomass. I hypothesized that reproductive strategy would be associated with the stress regime, where less stressed (more productive) plots produce a higher proportion of chasmogamous seed while more stressed (less productive) plots produce more cleistogamous ones.

Materials & Methods

The experiment was conducted within a recently restored emergent wetland in the Pond Brook Conservation Area of Liberty Metropark, Twinsburg, Summit County, Ohio (41°19’23.61”, -81°23’55.37” el. 303m). This restored wetland was chosen for its conservation relevance (wetland construction is commonplace in the region, and restored mineral-soil wetlands are likely to be the dominant wetland habitat type in the next century (see Chapter 5)) and because early successional communities are expected to be less resilient to climatic shifts than established communities (Grime et al. 2000). The restored marsh receives hydrologic inputs from the Aurora Pond dam outlet approximately 0.5 km to the East (41°19’30.42”, -81°23’34.51”) and drains South via a 0.34km shallow channel into Pond Brook with a slope of <0.1%.

At the experiment onset, approximately 4.7 of the 30 hectares (16%) of restored marsh were dominated by *Leersia oryzoides* comprising the western edge of the non-forested area (Figure 3.1). Portions of the marsh nearer to the Aurora pond outlet and within the historic drainage channel were dominated by *Typha angustifolia*. Field plots were established in Willette Muck, consisting of 81cm deep sapric material over poorly drained clay (USDA 2010). A bathymetry model was generated from 119 field measurements of surface water depth during the spring flood of 2011 to aid in site selection (Figure 3.1). Using this model, a 30mX66m area was selected that fell along a uniform East-West elevation gradient. Two 30m X 30m sampling grids were established, comprising a total of 36 plots spaced a minimum of 6 meters apart.

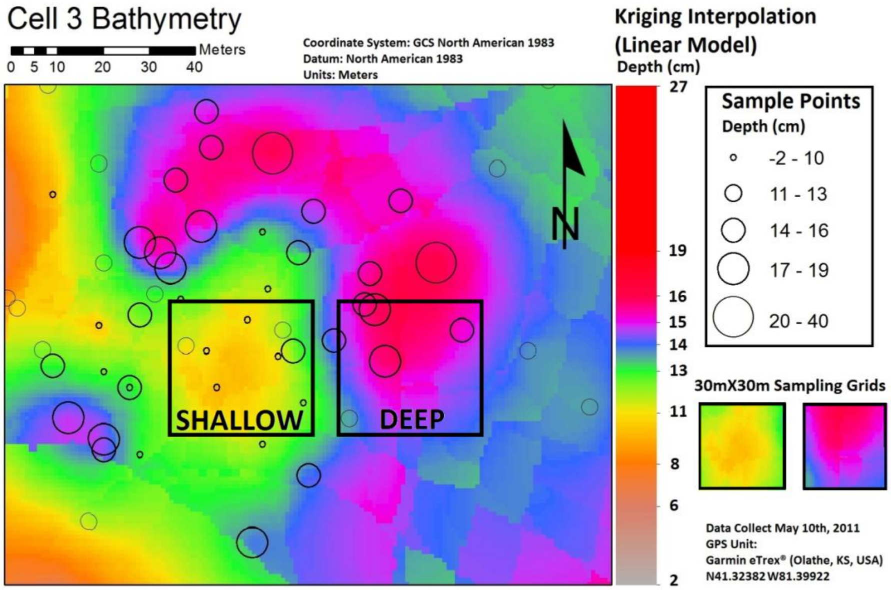


Figure 3.1. The above bathymetric surface was generated from surface water depth measurements taken during the spring flood of 2011 (n=119). Surface water measurements were stratified over a 6 hectare area (average nearest neighbor = 10m). Measurements were concentrated around the two 30m X 30m sample grids where measurements were separated by an average of 5 meters. The two hydrologic regimes exhibited a 7cm difference in mean surface water depth.

Climate manipulation was achieved through the construction of Open Top Chambers (OTCs) (Marion et al. 1997). OTCs were constructed using 5cm x 5cm x 100cm wooden stakes, driven in a 1.5m x 1.5m square, angled inwards for a 70° dihedral angle, then wrapped in Tufflite IV® greenhouse plastic to partially enclose a volume of 1.12m^3 (sensu (Carlyle et al. 2011)). Similar structures have proven effective at mimicking climate change in the form of a 1-6°C elevation in temperature at northern latitudes (Hollister & Webber 2000), and have recently been used successfully in mid-latitude marshes (Gedan & Bertness 2009). A structural control (SC) treatment was included (sensu Gedan & Bertness 2009) to account for potential artifacts imparted by the chamber. Structural controls were composed of wooden stakes wrapped with deer netting (1.5cm^2 mesh) to mimic the boundaries of the plastic structure. Un-manipulated controls were marked with survey flags. Plots were established such that all treatments were represented at each 6m increment along the hydrologic gradient (n=6 per 30mX30m sample grid). Plots were chosen to include *L. oryzoides*-dominated stands (n=36, $\bar{x}$=84% cover based on visual estimates) and surface water depths were recorded for candidate plots (Figure 3.2) to ensure the accuracy of the bathymetry model.

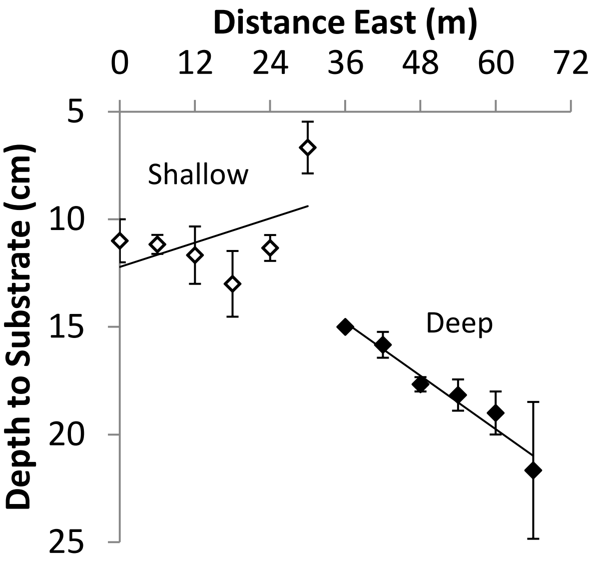


Figure 3.2. Experimental plot surface water depths recorded May 18th, 2011. Each point represents a mean of 3 plots (one for each treatment) and bars represent 2X Standard Error. Shallow (white) and Deep (black) hydrologic regimes. Lines represent linear best-fit (shallow R^2=0.25, deep R^2 = 0.95). With the exception of plots occurring at 30 meters East, mean plot values fell along a -0.16% eastward slope (R^2=0.92).

A subset of plots (n=4 per treatment) were instrumented with data-loggers (Thermochron iButton model DS1921G-F5, Embedded Data Systems Inc.) at 10cm above the soil surface that recorded temperature at one hour intervals during portions of the growing season. Data-logger records were used to calculate mean temperature, total degree days, and heat stress degree days (Chapter 2) and differences among treatments were analyzed via two-way ANOVAs followed by a sequential Bonferroni adjustment (Holm 1979) for multiple comparisons. Diurnal variation in temperature differences were compared among treatments via repeated measures ANOVA treating both depth and plot type as fixed factors. Analyses were conducted in JMP PRO 10 Statistics® (SAS Institute, Cary, NC).

Productivity

Net seasonal production was measured by harvesting all above-ground biomass from the central 0.25m^2 of each plot in September of 2012 which I then separated into thatch and living fractions. Samples were placed in paper bags, dried to constant weight at 60°C and weighed. Living and litter fractional biomass were compared separately for plot type and depth effects via two-way ANOVA (JMP PRO 10 Statistics®) following tests of heteroscedasticity and appropriate transformations. A sequential bonferroni correction was applied to avoid inflation of the type I error rate.

The Ratio Vegetation Index (RVI) (Pearson & Miller 1972) was calculated for all plots at 9 time-points throughout the growing season and used to test for treatment effects on the timing of production. RVI has been used as proxy for the amount of vegetation per unit area (Pearson & Miller 1972), and represents one of the earliest and most frequently used vegetation indices (Jackson & Huete 1991). Although many vegetation indices have been developed since RVI (e.g. NDVI, SAVI, etc…), RVI was chosen for its sensitivity when vegetation density is high (Jackson & Huete 1991). The system studied here was characterized by rapid accumulation of vegetation in the spring and high vegetation density in early June when heat stress events were hypothesized to be most frequent. A time-weighted average of RVI values (a proxy measure of peak biomass) was compared among plot types and water table depths via two-way ANOVA and treatment affects on seasonal variation in RVI were analyzed via repeated measures ANOVA. Analyses were conducted using JMP Pro 10® Statistics software. Treatment differentials from un-manipulated controls were compared via quartic (4th order polynomial) regression, as the quartic function best approximates the hypothesized difference in productivity for a single growing season (Chapter 2, Figure 3.2.1).

Calculating the Ratio Vegetation Index (RVI)

RVI represents the ratio of near infrared reflectance (760-900nm) and red reflectance (630-690nm), which were measured between March-August using a TetraCam ADC® multispectral digital camera (Tetracam Inc. Chatsworth, CA). Plot photos were taken from a leveled mount 1.4m above the soil surface at the center of each plot (comprising 0.81m^2 or 36% of plot area coverage at the soil surface). Multispectral images were color-processed using TetraCam PixelWrench2® software and individual reflectance values extracted using ImageJ® (Rasband 1997). NIR reflectance is strongly associated with area of functioning mesophyll while far red reflectance is an inverse indicator of foliar chlorophyll content (Broge & Leblanc 2001; Carter & Knapp 2001). The ratio vegetation index (RVI) calculated as the ratio NIR/Red (Pearson & Miller 1972) was used to combine proxies of foliar area and chlorophyll content (Tucker 1977) into a single estimate of instantaneous production. For a discussion of correlations between vegetation indices and production see Christensen & Goudriaan (Christensen & Goudriaan 1993).

Morphology and Reproduction

Leersia oryzoides were collected from each sample plot (n=6 per plot) in September 2012 (approximately 1 week following chasmogamous fruit maturation).

Ramets were selected at random from the central $0.25m^2$ of each plot, and length from substrate to apex was recorded with a meter stick. Ramets were collected and $44mm^2$ leaf punches (n=5-10) were taken immediately from the most recent fully expanded leaf. Samples were returned to the lab and dried to constant weight at 60°C before processing. Dried leaf punches were counted and weighed. Mean ramet height and mean specific leaf area (calculated as $44mm^2 \div$ average leaf punch mass per ramet) were compared via two-way ANOVAs following appropriate tests for heteroscedasticity and normality.

Leersia oryzoides produces generally chasmogamous flowers in its apical inflorescence. Most ramets (93% in this study) also produce functionally cleistogamous flowers enclosed between the leaf sheath and the culm in the internodes below the apical inflorescence. Caryopses (hereon referred to as seeds) were collected from the apical and axillary inflorescences and weighed separately. Seed were counted using the particle analyzer function in ImageJ® (Rasband 1997) after appropriate color threshold processing and binarization. Welch's Tests were used to compare the ratio of CH/CL seed produced per ramet among depths and plot types (owing to heteroscedasticity that was robust to transformation)(JMP Pro 10® Statistics software) and a Sequential Bonferroni (Holm 1979) was applied to account for repeated measures. Subsequent two-way ANOVAs were performed to assess the effects of depth and plot type on seed mass and resource allocation to reproduction treating CH and CL independently and in combination. A Sequential Bonferroni adjustment (Holm 1979) was applied to these analyses to avoid inflation of type I error. Finally, Fisher's Exact Tests (Fisher 1922) were used to determine whether significant shifts in the CH/CL ratio led to significant differences in the predominant seed type produced (CL vs CH) per ramet.

Community composition

Although plots were largely dominated by *Leersia oryzoides* at establishment and throughout the growing season of 2011, the site saw considerable turnover in 2012. Deep plots that were dominated by Leersia in 2011 were dominated by *Bidens aristosa* in 2012. As a result, a modified point-intercept method (Jonasson 1988) was used to assess final compositional differences among plots (August 2012). An 8mm diameter pin was passed vertically through the vegetation at 10 randomly selected locations within the central $0.25m^2$ of each plot (to minimize edge effects). The species identity and height for the top 4 contacts were recorded for each pass, equating to a maximum of 40 contacts per plot. Relative abundance was estimated as the percentage of total contacts by each species, and species with no contacts were assumed to have a relative abundance <2.5%. A two-way ANOSIM was conducted in PAST (Hammer et al. 2001) to compare plot-level community dissimilarity (in terms of Bray-Curtis dissimilarity coefficients) among plot types and depths. SIMPER analysis (Clarke 1993) was employed to order species in terms of their relative contribution to community differences.

Results

Two-way ANOVAs with depth and plot type as fixed factors and mean temperature, total degree days, and accumulated heat stress degree days (March-September) as dependent variables were significant (Table 3.1). Shallow plot means were significantly higher than those of deep plots but plots did not differ significantly by structure type (Table 3.1), although a combination of a small sample-size and inter-plot variability may have yielded insufficient power to detect differences.

Table 3.1. Two-Way ANOVA results and effect tests for Mean temperature (°C), Total Degree Days (TDD) = $\sum_{4.4°\mathrm{C}}(Tobs - 4.4°\mathrm{C}) * Time$ and accumulated heat stress degree days (HSDD) = $\sum_{35°\mathrm{C}}(Tobs - 35°\mathrm{C}) * Time$. The ($\dagger$) symbols indicate significance following sequential bonferroni correction (Holm 1979) and ($\ddagger$) symbols indicate factor effect significance. Depth X Plot Interactions were not significant and therefore left out of the model (not shown).

Source	**DF**	**F**	**P**	**Power**
Mean Temp	*3,22*	*4.3526*	*0.015†*	
Depth	1	7.5366	0.0118‡	0.7466
Plot Type	2	2.2768	0.1263	0.4128
TDD	*3,22*	*3.88*	*0.0229†*	
Depth	1	6.5863	0.0176‡	0.6891
Plot Type	2	2.2722	0.1268	0.4121
HSDD	*3,22*	*5.0412*	*0.0083†*	
Depth	1	12.4378	0.0019‡	0.9206
Plot Type	2	0.8205	0.4533	0.1722

Temperature records revealed apparently opposite effects for open top chambers in shallow vs deep plots (Appendix B.1). Shallow plots with chambers exhibited a 40-50% increase in accumulated heat stress degree days relative to controls, while OTCs established in deep plots exhibited a 62% decrease in accumulated heat stress degree days (Appendix B.1). See Appendix B.2 for traditional degree day accumulation curves. Temperature deviated most from controls between 1PM and 4PM EST (Figure 3.3), but did not differ significantly among treatments (repeated measures ANOVA $F_{3,20}$=0.73, p=0.5).

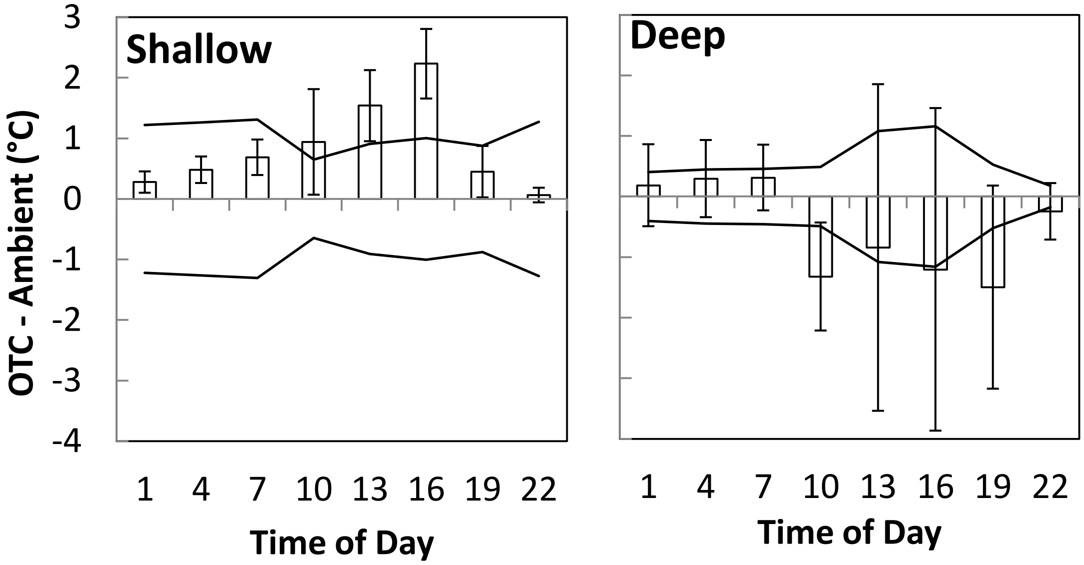


Figure 3.3. Mean OTC differences from controls (bars). Error bars represent 2X SE for OTC means (n=4) while thin lines represent 2X SE for UC means.

Two-way analyses of variance with depth and plot type as independent variables and living and litter biomass fractions as dependent variables were significant ($F_{1,29}$=4.4/3.3, p=0.01/0.035 respectively)(Sequential Bonferroni applied). Deep plots accrued significantly less living biomass than shallow plots ($F_{1,29}$=10.95, p=0.008), but living biomass did not differ by structure type ($F_{3,29}$=1.08, p=0.59) (Figure 3.4). Litter biomass was unaffected by depth ($F_{3,29}$=0.05, p=0.8), while control plots accrued significantly less litter than plots with chambers (based upon Tukey's HSD pair-wise comparisons). Depth X treatment interactions were not significant for either litter or living biomass fractions and were therefore left out the models.

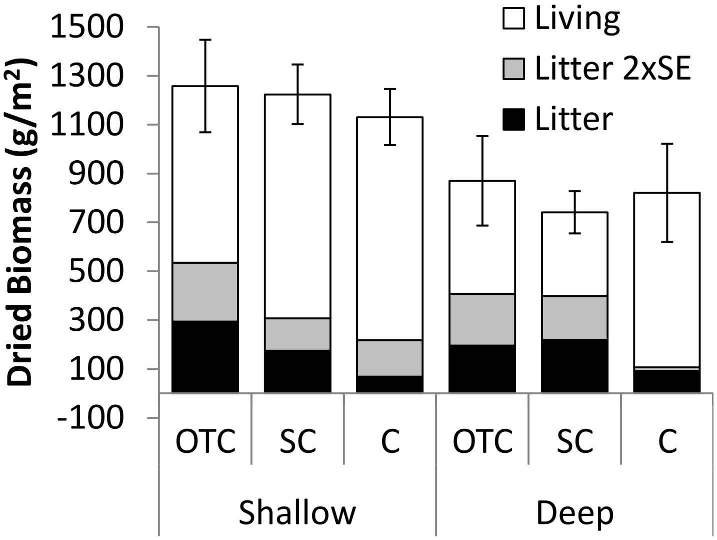


Figure 3.4. Biomass collected in September 2012 for plots established in 2011. Total bar length represents total mean biomass (litter + living). Black and grey bars represent litter and litter error values (respectively).

A repeated measures ANOVA with depth and plot type as independent variables and RVI observations as dependent variables was significant ($F_{5,14}$=6.6, P=0.004). Between-subjects comparisons revealed plot type to have a significant effect on RVI response ($F_{2,14}$=8.3, P=0.003) but not depth ($F_{2,14}$=4, P=0.06). Plot type X depth interactions were not significant ($F_{2,14}$=2.6, P=0.1), and were therefore left out of the model.

A two-way ANOVA with depth and plot type as independent variables and weighted mean RVI (a productivity proxy) as an independent variable was significant ($F_{5,14}$=5.79, p=0.004). Plot type X depth interactions were not significant ($F_{5,14}$=2.9, p=0.087). Weighted RVI values were larger for shallow plots than for deep plots, but these differences were not significant ($F_{5,14}$=0.56, p=0.47). Although OTCs yielded the largest declines in productivity proxies relative to control plots, both OTC and SC chamber types reduced productivity significantly (post-hoc analysis via Tukey's pair-wise comparisons). These differences in RVI were most pronounced in June (Figure 3.5).

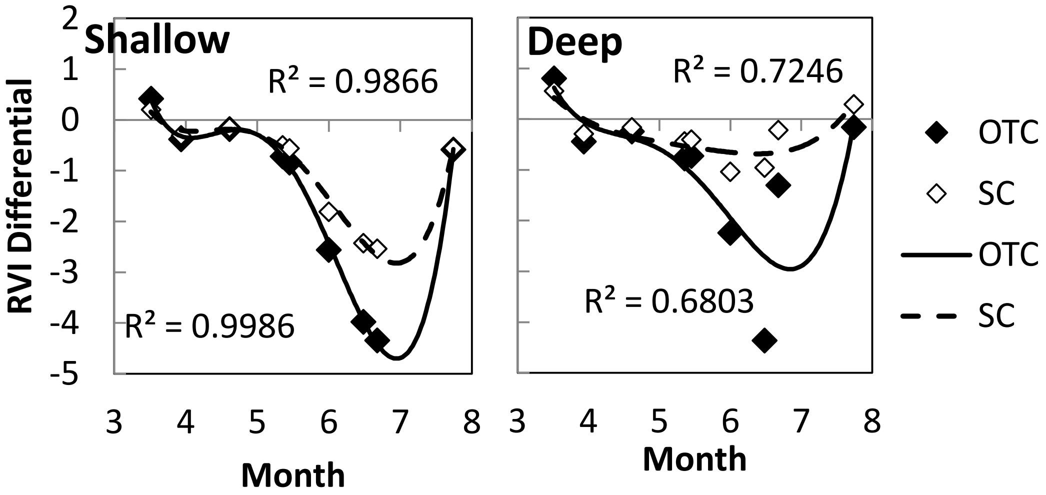


Figure 3.5. Differences in the Ratio Vegetation Index (OTC-UC and SC-UC) for the 2012 season. Each point represents the difference in means between treatments (n=6). Lines represent 4th order polynomial functions fit to OTC (solid line) and SC (dashed line) values and R^2 values represent the proportion of variation explained by these functions (SC above, OTC below).

Functional Response : Reproduction

Specific leaf area ($\bar{x}$=220cm^2/g) did not differ with respect to depth or treatment ($F_{3,27}$=0.5, p=0.7). Mean ramet height was significantly reduced in deep plots ($F_{3,27-}$=9,9246, p=0.004) but did not differ significantly by treatment ($F_{3,27}$=0.4, p=0.7). See Appendix B.3 for Two-way ANOVA results. Despite a significant effect of depth on ramet height, there were no discernible allometric relationships between ramet height (a proxy for individual-level biomass) and seed mass/ramet or the CH/CL ratio (log-log regression $F_{1,59}$=0.6/0.06, p=0.4/0.8 respectively). A two-way ANOVA with plot type and depth as independent variables and the CH/CL ratio as the dependent variable was significant ($F_{3,26}$=5.9568, p=0.003), but violated ANOVA assumptions of homoscedasticity (Bartlett Test F=3.98, p=0.046). Welch's tests were applied as an alternative to assess main effects, which indicated a significant effect of depth (F=37.37, p<0.0001), but not plot type (F=0.32, p=0.8)(Figure 3.6).

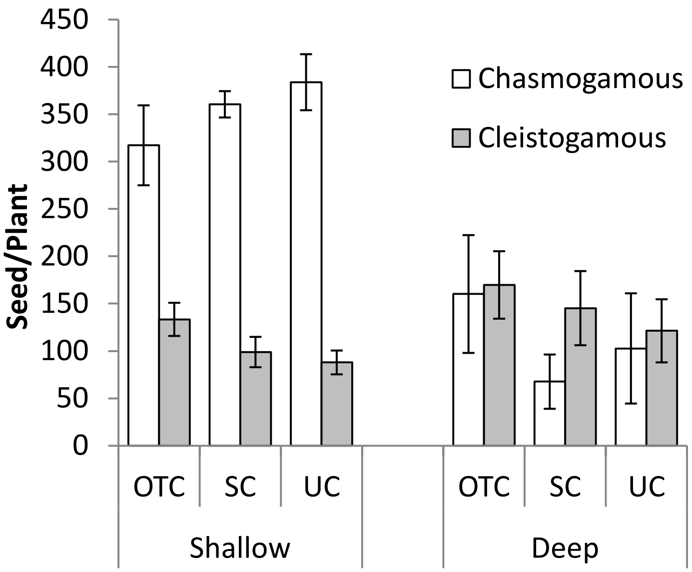


Figure 3.6. A comparison of chasmogamous versus cleistogamous seed produced per ramet by depth and plot type. Error bars represent 2X standard error. Two-way ANOVAs indicated significant differences in chasmogamous seed production for depth but not plot type.

Further, a Fisher's Exact Test indicated that propagule type shifted from predominantly chasmogamous to cleistogamous seed when transitioning from shallow to deep plots (χ^2=7.6 p=0.01)(Figure 3.6). Multiple two-way ANOVAs indicated that these effects were largely the result of modulation in the number of CH seed produced per ramet (Appendix B.3.), while CL number did not vary appreciably among treatments (Appendix B.4). Cleistogamous seeds were significantly more massive (0.08 mg vs 0.04 mg) than chasmogamous ones (F=3.13, p=0.008).

Community Metrics

Leersia oryzoides prevalence declined at the site in August 2012, subsiding to dominance by *Bidens aristosa* in deep control plots (Appendix B.5). Chambers exhibited a greater coverage *of L. oryzoides* when compared to controls (LS Means Contrasts $F_{1,30}$=7.27, p=0.011). A two way ANOSIM (Clarke 1993) detected significant differences in the relative abundance of community constituents (Bray-Curtis dissimilarity) in terms of plot type (OTC/SC/UC n=12/11/11 R=0.154, p=0.0112) and hydrology (Shallow/Deep n=18/16, R=0.383, p=0.0002). SIMPER analysis (Clarke 1993) identified *Polygonum pennsylvanicum* and *Bidens aristosa* as most responsible for differences in observed dissimilarity (Appendix B.6).

Discussion

Chamber effects on temperature were small relative to the natural differences in temperature between depths. Shallow plots were significantly warmer than deep plots (+1°C), and exhibited a 4-fold increase in accumulated heat stress degree days which likely resulted from differences in evapotranspiration rates and differences in the frequency of data-logger inundation. Open top chambers yielded increases in temperature between +0.15°C and +0.34°C above ambient, but these differences were not significant. Carlyle et al. (2011) used the same chamber design (inspired by Marion et al. (1997)) which yielded non-significant increases in mean temperature of +0.2°C above ambient. Similar chambers used by Marion et al. (1997) yielded temperature increases of 0.62°C. In this study, the greatest temperature differentials associated with OTCs were generated in the early afternoon just after peak irradiance (between 1PM and 4PM), which is consistent with the findings of both Marion et al. (1997), and Carlyle et al. (2011). In shallow plots, stressful heat events were 39% more intense/frequent in

OTCs than in controls, consistent with studies that evaluated the impacts of OTCs on temperature maxima using various metrics (Suzuki & Kudo 1997; Bokhorst et al. 2013). It is valuable to note that De Boeck et al. (2012) recently demonstrated that leaf temperature differentials between OTCs and control plots were twice as large as air temperature differentials, owing to wind impedance. This suggests that ramets within OTCs likely experienced a greater extent of warming and a higher incidence of heat stress than control plots in this study, despite a lack of significant divergence in recorded air temperatures.

Peak biomass was limited in deep plots relative to controls, indicating a more stressful condition, while seasonal timing of instantaneous production yielded depressions in OTC productivity owing to an increase in thatch retention (Figure 3.5). Open top chambers did not alter accumulated biomass appreciably, though they did accumulate thatch (predominantly in the form of senesced *L. orzyoides* culms) faster than un-chambered plots. This layer of thatch was evident after a single season of manipulation (pers. obs.) and, in addition to community turnover in deep plots, may have contributed to the observed differences in productivity. Deep plots were arguably more stressful than shallow plots based upon peak living biomass (Figure 3.4). This is consistent with other studies that have demonstrated a negative relationship between plant production and water table position (Fraser & Karnezis 2005). However, depth did not affect instantaneous production, a metric that is sensitive to transient stress in leaf tissues (Chapter 2;Carter & Knapp 2001), suggesting that while depth increased the net amount of stress experienced by the vegetation, chambers affected the timing of production and decreased productivity coincident with the warmest part of the 2012 growing season (NOAA 2012). Productivity shifts induced by OTCs likely arose from a thicker layer of thatch in the spring that restricted early emergence, and possible increases in heat stress accumulation.

The presence of OTCs or increased mean water table depth was expected to affect morphology in ways that were indicative of increasing stress. *Leersia oryzoides* individuals were shorter in deep plots, consistent with the idea that water-logging stress limits productivity (Soukupová 1994; Blom & Voesenek 1996; Jackson & Colmer 2005). However, this difference in apparent growth may have been affected by the overtopping of plots by *Bidens aristosa* and *Polygonum pennsylvanicum* in the summer of 2012. *Leersia oryzoides* individuals collected before this invasion in 2011 were also significantly shorter in deep plots by 26%, suggesting that these plots were 'chronically unproductive' (Keddy 2002) (i.e. stressful (Grime 1977,1979)). Specific leaf area, an inverse measure of resource allocation per unit photosynthetic area, is thought to differentiate between individuals occurring in high versus low stress environments (Grime 1979,2001; Westoby 1998; Wilson et al. 1999). Specific leaf area did not differ among treatments, which was consistent with Suzuki et al. (1997), who detected little change in SLA as a result of warming via OTCs for a variety of species in northern Japan. Considerable variability in SLA among ramets (values ranged from 119 to >350cm^2/g) may have played a role in this lack of difference.

It has been hypothesized that dimorphic (facultative) cleistogamy is an adaptation for more efficient allocation of resources use in variable environments

(Cheplick 2007). The most drastic treatment effects came in the form of significant shifts in resource allocation to chasmogamous reproduction as a function of depth. Water-logging stress was associated with a shift to producing fewer chasmogamous seed. This shift in reproductive strategy has a number of implications for a future where climate change alters stress on a continental scale.

Control conditions suggest that seed produced along the upland portions of the hydrosere were predominantly out-crossed while seed from more frequently submerged ramets were predominantly selfed. Culley et al. (2007) suggested that heteromorphy between cleistogamous and chasmogamous seed may also yield differences in dispersal ability, where CL seed serve to maintain a robust seed bank at the maternal site while CH seed are more capable of dispersal. *Leersia oryzoides* collected in this study support this notion. Chasmogamous seed were significantly less massive than cleistogamous seed, providing greater opportunities for dispersal in surface waters. Furthermore, CH seed are born in terminal panicles, and almost all CH seed disarticulate before October. In contrast, cleistogamous seed born from axillary inflorescences remain within the senesced culm, limiting their dispersal to the immediate vicinity of the maternal ramet (Campbell et al. 1983; Cheplick 2007).

OTCs appeared to increase the amount of cleistogamous seed produced in shallow plots (though not significant), suggesting that an increase in thatch yielded sufficient stress to induce shallow ramets to more resemble deep ones in reproductive strategy. Where somewhat drier conditions offered a refuge and potentially a favorable condition for outcrossing in *Leersia oryzoides*, climate change may restrict this avenue of reproduction for *L. oryzoides* and other cleistogamous grasses. Where outcrossing (though infrequent) contributes to the adaptive capacity of *L. oryzoides* and other dimorphically cleistogamous species (Campbell et al. 1983; Schoen & Lloyd 1984), pervasive stressful conditions brought about by climate change may yield a future where populations become more limited in the range of reproductive strategies they employ.

Chambers (both OTCs and structural controls) resisted invasion by *Bidens aristosa*, initially suggesting that chamber effects must be considered as a combination of augmented thermal stress and a decrease in interspecific competition. If chambers restricted competition between *L. oryzoides* with its neighbors, it might be expected that stress would decline in these plots relative to similarly positioned controls, yielding results that would appear to discount our hypothesis. However, *L. oryzoides* ramets growing as subdominants in control plots were in fact less stressed than those occurring in OTCs, evidenced by higher CH/CL ratios, which could be the product of a combination of mechanisms that cannot be disentangled without further experimentation. First, despite shifts in community structure, *L. oryzoides* responses may have been most directly affected by the hydrology and temperature and interspecific competition was not an important differentiating factor among treatments. Second, facilitation may have been more pronounced in the community found in deep plots (which was compositionally dissimilar to that of shallow plots), yielding augmented production in *L. oryzoides* ramets. Finally, conspecific density and accumulated thatch may simply be more stressful to emerging *L. oryzoides* ramets than the presence of interspecific competitors in waterlogged plots.

Although the responses of native populations to climate change may be subtle in the near term, pervasive shifts in reproductive mode may yield major changes in meta-population dynamics. Increasing isolation of grass populations could limit exchange of genetic material throughout species ranges, limiting the ability of these species to successfully adapt to further environmental change.

Acknowledgements

I would like to thank the University of Akron Departments of Biology and Geography & Planning for providing facilities and technology for this experiment, Summit County Metroparks (special use permit issued May 7th, 2010) for access to the field site, and Choose Ohio First Tiered Mentoring and Bioinformatics Scholarship programs for providing resources and personnel for this project. I would like to thank John “Tony” Miller, Jessica LaHurd, and Caitlyn McClendon for their valuable efforts in sample processing and I would also like to personally thank the many field assistants who have helped on this project, including Sean Kelly, Lindsey Steinwachs, Zachary Haake, and the 2011 Field Ecology Class. Finally, I would like to thank the University of Akron Field Station for providing facilities and a pickup truck for transportation to and from field sites.

CHAPTER IV

WETLAND COMMUNITY RESPONSES TO INCREASES IN FLOODING AMPLITUDE AND FREQUENCY

Abstract

Climate simulations predict an increase in both the amplitude and frequency of flooding events in the American Midwest. I tested the effects of increasing hydrologic variability on wetland productivity, community assembly and functional traits. Wetland mesocosms comprising a mixture of native hydrophytes were established over a single growing season and subjected to hydroperiods with two different amplitudes and frequencies the following summer. High amplitude/frequency hydrologic regimes yielded communities with a larger proportion of forbs than controls. Increasing hydrologic variability produced communities with greater within-group variance, and a larger compositionally-weighted specific leaf area. These results suggest that community assembly will follow less predictable patterns under a changing climate and communities may become more open to colonization.

Introduction

Hydrology is the primary driver of community composition and ecosystem functioning in wetlands (Keddy 2002). Wetlands persist within thresholds of flooding amplitude and frequency, where flooding of low amplitude and frequency leads to incursion of upland species, and high-amplitude/frequency flooding restricts most macrophyte species from persisting (Nilsson 1981). Shifting precipitation patterns resulting from climate change will likely have pervasive impacts on the composition and distribution of wetland communities. Climate simulations for the Midwestern United States indicate that wetlands will be subjected to both increases in flood depth due to intense rainfall events and increasing water stress due to augmented evaporative potential in a warmer world (USGCRP 2009). This had led many to predict that wetlands with historically persistent, mild flooding will be subjected to greater hydrologic variability (Mortsch 1998; Wuebbles & Hayhoe 2004; Erwin 2009; USGCRP 2009). This variability will likely have pervasive impacts on the structure and function of wetland communities in the near future.

A major goal of vegetation science has been to encapsulate the associations between plant communities and the environments where they are typically found (e.g. stressful-benign, variable-static) within a single theory (Lavorel et al. 1997; Westoby 1998; Craine 2009). Of the many theories that have been proposed, most link measurements of tradeoffs in plant morphology (functional traits) to surviving environmental adversity rather than a focus on phylogenetic relationships (Korner 1994; Westoby 1998; Westoby 1998; Hodgson et al. 1999; Dormann & Woodin 2002; Sonnier et al. 2010). Grime proposed one such theory (CSR Theory) by grouping vegetation into three categories based on trait similarities found along gradients of stress and disturbance (Grime 1977;1979;2001). Species that proliferate under benign conditions (low-stress and low-disturbance) were thought to exhibit traits associated with competitive ability (increased canopy height, seed mass, and specific leaf area (Westoby 1998)). Species that performed well in stressful environments expressed traits associated with the preservation of vegetative tissues (increased leaf longevity, decreased stature and specific leaf area). Finally, species in frequently disturbed environments expressed traits associated with regeneration (short-lived, low seed mass, high seed number). This model and subsequent derivations have been successfully applied at the local and regional scale under a variety of environmental contexts. Some of the most recent applications of CSR-type models have predicted shifts in traits as a function of climate at large spatial scales (Swenson & Weiser 2010; Schmidtlein et al. 2012) and have been used to predict which environments can support the greatest number of species (Le Bagousse-Pinguet et al. 2013).

An inherent challenge to applying CSR theory involves framing variation in a factor (i.e. hydrology) in model terms (stress and/or disturbance). Increasing hydrologic variation in the manner described above yields increases in both the frequency and amplitude of water table fluctuations within a single growing season. Within a limited range, an elevated water table can yield increases in habitat-level productivity (Keddy 2002). Outside of that range, flooding and drought can stress wetland plants, and at greater intensities leads to the destruction of plant tissues (disturbance), yielding considerable variability in wetland productivity (Brinson & Lugo 1981). Ambient conditions in Midwestern mineral-soil wetland include prolonged flooding and intermittent periods of soil surface exposure, with floods of sufficient magnitude to uproot or destroy plant tissues occurring on annual to multi-decadal cycles. These habitats maintain relatively high productivity, and are generally dominated by species possessing traits associated with a compromise between stress tolerance and competitive ability (C-S strategists).

Figure 4.1 presents a simplified model that predicts how the stress-disturbance regime will shift from low to high hydrologic variability (see Appendix C.1 for a more generalized model). Increasing hydrologic variation leads from generally benign conditions, to predominantly stressful, to predominantly disturbed conditions.

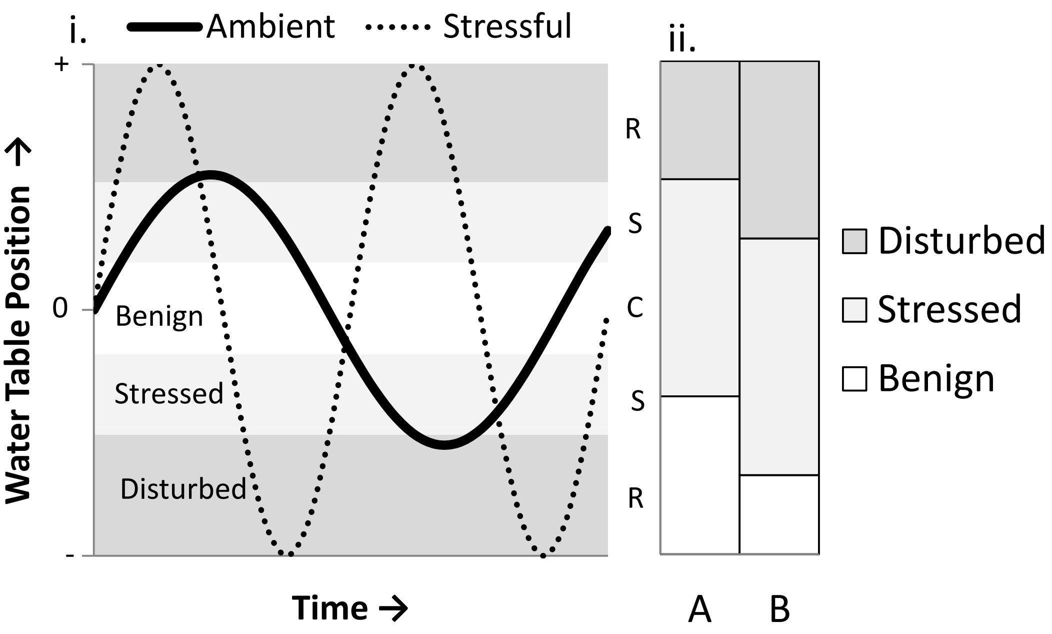


Figure 4.1. This conceptual model describes the effects of simultaneously increasing water table amplitude and frequency on the stress-disturbance regime. Rising amplitude and frequency bring vegetation in contact with three classes of environmental adversity consisting of

conditions that are benign—productivity would be maximized in monoculture, stressed—growth is suboptimal, or disturbed—plant tissues are removed or irreversibly damaged. Grime's CSR strategies favored by each adversity class are indicated on the right edge of i. (ii.) presents the integrated proportion of time each hydrologic regime produces the three classes of environmental adversity (vertical) which is in principle proportional to the selection intensity for each of the three strategies outlined in CSR theory.

Based on this model, future wetlands will exhibit shorter periods of optimal production, an increased duration of stress, and an increased duration of flooding and drought of intensities great enough to destroy plant tissues. As a result, I hypothesize that increases in hydrologic variation will lead to a decrease in community-aggregated traits associated with competitive ability, as conditions favor species with traits associated with regeneration or tolerance (R or S strategists). This decrease in the importance of competition yields several predictions about future communities based on elaborations of the CSR paradigm. Decreasing competition should increase diversity, as communities incorporate species intermediate to all three major strategies (Le Bagousse-Pinguet et al. 2013). The resulting community composition will be less predictable, as recruitment or survival depend on micro-scale variations in seed dispersal and light infiltration to the soil surface. A decline in the importance of competition will yield communities with a lower canopy (as increasing canopy height would offer little selective advantage), a decrease in seed mass (as disturbed conditions favor dispersal ability over resource provisioning), a decrease in leaf dry matter content, an increase in seed production, and an increase in specific leaf area. Specific leaf area (SLA) is strongly associated with resource allocation to rapid colonization of light gaps that is thought to be a tradeoff with leaf longevity (Wilson et al. 1999). Conditions in the understory should favor species with an increased SLA allowing rapid colonization of light gaps, while conditions in the established community should favor a decrease in SLA reflecting an optimization to a less productive environment.

Materials & Methods

A total of 20 wetland mesocosms were generated in stock tanks (379 liters) on a leveled pad at the University of Akron Field Station (Summit County, Ohio, USA) in 2011. Mesocosms included 57 dm^3 of rounded river stones (10-13mm diameter) as a drainage substrate, and were then filled to within 30cm of the rim with native muck collected from an impacted wetland (N41.558401,W81.592871) comprising a surface area of 1 m^2 for plant community development (Mesocosms were similar to those described by Ahn and Mitsch (Ahn & Mitsch 2002)). Water tables were manipulated and maintained via a linked pair of standpipes where vertical pipes received 2 liters/hour of water as needed through drip emitters during the growing season and overflow pipes established the appropriate water table depths. Source water was pumped from a nearby pond and gravity fed via drip emitters to mesocosms from a 6000 liter reservoir.

Mesocosms were seeded with 8.5g m^{-2} (20X the recommended seed density for restoration applications) of a mix of 29 native wetland species (Spence Nursery Inc. Emergent Wetland Mix) in July of 2011 and again in January 2012 (5.5g). The effects of water table fluctuation on recruitment and seedling survival are well established (Fraser & Karnezis 2005). Therefore, water table depths were maintained at 2cm below the soil surface until seedlings had established and overwintered to minimize the influence of chance events leading to inter-plot heterogeneity.

In June 2012, two hydrologic regimes were established using nearby groundwater fluctuations as a guide for the number and periodicity of flooding events. Ambient water table fluctuations were estimated as a function of the number and amplitude of flood peaks recorded in a nearby USGS observation well (USGS 404655081553100 WN-8). I identified 39 'flood' events during a concurrent period the previous year (June-September) with mean amplitude of 7 cm and mean cycle duration of 19 days. Standpipes on mesocosms were manipulated so that the ambient treatment was subjected to water table fluctuations with amplitudes of 6cm and mean cycle durations of 22 days, while the stressful treatment water tables received amplitudes of 12cm and mean cycle durations of 14 days.

Multispectral remote sensing can be used to generate non-destructive proxies of productivity at multiple time-points (Pearson & Miller 1972; Jackson & Huete 1991). Reflectance in the visible and near infrared (NIR) spectral bands was recorded at regular intervals throughout the 2012 growing season (March-October) using a TetraCam ADC® multispectral digital camera (Tetracam Inc. Chatsworth, CA). Photos were taken from a leveled position 1.4m from the soil surface, encompassing 0.8m^2 of each mesocosm. Photos were processed in TetraCam PixelWrench2® software and 8 bit reflectance values extracted using ImageJ®. NIR reflectance is strongly associated with area of functioning mesophyll while far red reflectance is an inverse indicator of foliar chlorophyll content (Broge & Leblanc 2001; Carter & Knapp 2001). The ratio vegetation index (RVI) calculated as the ratio NIR/Red (Pearson & Miller 1972; Christensen & Goudriaan 1993) was used to combine proxies of foliar area and chlorophyll content into a single estimate of instantaneous production (See Chapter 2 Methods for a more in-depth discussion this metric). Ratio vegetation indices were compiled by treatment and date, and analyzed by way of repeated measures analysis of variance using JMP 10 PRO® Statistics (SAS Institute, Cary, NC).

Community composition and relative abundances were measured following two methods in October, 2012. First, the relative cover of each macrophyte species present was estimated visually for each plot by recording the identity of each species and estimating fractional contribution of each species to total cover (Greig-Smith 1983). Second, composition, abundance, and canopy position/density were estimated following a modification of the point-intercept method (Jonasson 1988) in October of 2012. An 8mm diameter pin was passed vertically through the vegetation at 10 randomly selected locations within the central $0.25m^2$ of each plot (to minimize edge effects). The species identity and height for the top 4 contacts were recorded for each pass, equating to a maximum of 40 contacts per plot. The average maximum contact height was used as a proxy for comparisons of relative canopy height, as it reflects a threshold value above-which plant material is less dense, and light attenuation is likely decreased (pers. obs.). Canopy density was estimated as the average of the range of heights recorded (n=10). Relative abundance was estimated as the percentage of total contacts by each species, and species with no contacts were assumed to have a relative abundance <2.5%.

Community-aggregated functional trait values were derived by weighting species-level estimates of specific leaf area, mature height, number of seed per culm, and seed mass by their relative abundance in each mesocosm. Species-level trait values were compiled (congeners were used where species-level data were unavailable) from the literature (Farnsworth & Meyerson 2003) and public trait databases (United States Department of Agriculture (USDA) 2001). Trait variances were compared via multiple Levene's tests, and trait means were compared using separate F-tests. Welch's tests were used in cases where Levene's tests indicated significant heteroscedasticity.

Finally, all above-ground biomass was collected from the central $0.25m^2$ of each plot in October of 2012. Samples were placed in paper bags, dried to constant weight at 60°C and weighed. Treatment biomass/$0.25m^2$ was compared via a t-test.

Treatments were analyzed for between-group compositional dissimilarity via ANOSIM conducted in PAST (Hammer et al. 2001), and for heterogeneity of multivariate dispersion using the FORTRAN program PERMDISP (Anderson 2004). Similarity percentages (Clarke 1993) were evaluated in instances where ANOSIM yielded significant community divergence to identify which species were most responsible for the observed shift in community structure.

Results

The Ratio Vegetation Index (RVI) represents an approximation of the amount of incident radiation being used to drive photosynthesis, combined with the amount of living plant tissue to give an estimate of the instantaneous rate of productivity of a sample plot. As an illustration of this concept, a simple time-weighted mean of RVI over the 2012 growing season was significantly associated with peak accumulated biomass (Linear Regression $F_{1,18}$=37.22, p<0.0001)(Figure 4.2).

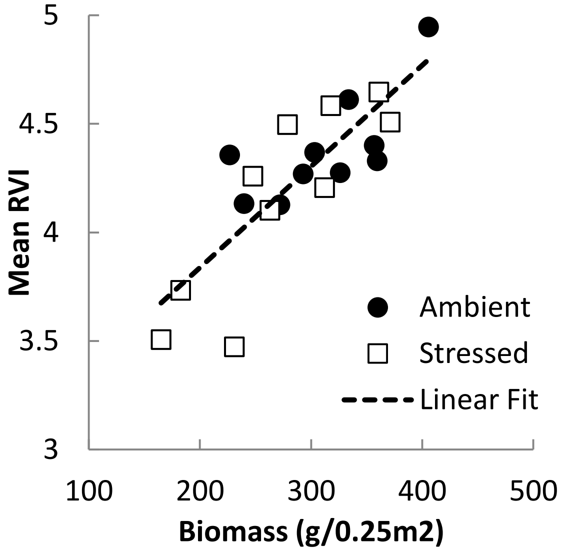


Figure 4.2. Mean RVI values for the period May-October 2012, were strongly correlated with biomass (dried) in October 2012.

Measured RVI differed significantly between ambient and stressful hydrologic regimes during the Spring of 2012 (repeated measure ANOVA, $F_{1,18}$=4.413, p=0.05), where the stressful treatment accrued biomass more slowly in the Spring than the ambient treatment (Figure 4.3) leading to a 7% decrease in cumulative RVI. However, the stressful treatment reached peak foliar cover at the same time-point as the ambient treatment in June, and no differences were discernible for the remainder of the growing season. It is important to note that observed differences in RVI occurred in April-May, before the onset of experimental variation in water table depth (June).

The stressful hydrologic regime yielded a 12% decrease in total accumulated biomass, but this difference was not significant (n=10, t=1.3697, α 1-tailed p=0.0938), possibly owing to insufficient power (Power=0.25). Estimates of canopy height and canopy density did not differ significantly between treatments in October 2012 (n=10, α 2-tailed t=-0.2 & -0.4 p=0.8 & 0.7 respectively).

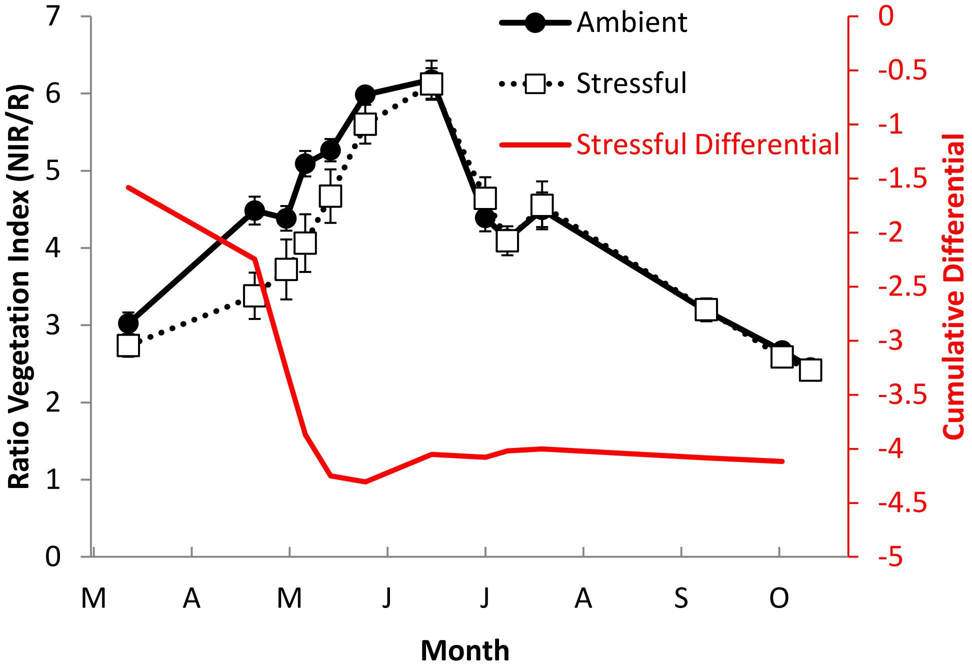


Figure 4.3. 2012 Productivity. Symbols represent mean RVI values (n=10) while error bars represent 2X standard error. Black lines represent raw (unadjusted) values for ambient (solid) and stressful (dotted) treatments. A cumulative differential curve is represented on the right-most y-axis (red), indicating the added difference between ambient and stressful treatments over time. RVI failed to increase as rapidly in the early season for treatments subjected to variable hydrology.

All mesocosms were dominated by the sedge *Carex lurida* with an average estimated contribution to above-ground cover of 59% (based on visual estimates), and comprising 73% of canopy cover (via the point-intercept method). Although visual estimates yielded generally more even communities than the point-intercept method (consistent with Greig-Smith (1983)), survey methods were in general agreement with respect to order of prevalence, and the direction of mean differences between treatments (visual estimation and point-intercept methods consistently showed the same direction of differences for 75% of the species evaluated).

The stressful hydrology treatment led to a 25% increase in the prevalence of forbs relative to graminoids in these otherwise graminoid-dominated communities (α 2-tailed t=2.4, p=0.03) (Figure 4.4). Forb composition differed significantly among treatments (Bray-Curtis ANOSIM R=0.13, p=0.025) while there was no discernible difference among plots in relative cover of graminoids (Bray-Curtis ANOSIM R=0.002, p=0.42). Post-hoc analysis via similarity percentages indicated that differences in the abundance of 4 species explained 76% of the observed dissimilarity (determined via Bray-Curtis coefficients). The stressful hydrologic regime exhibited a 29% decrease in *Boltonia latisquama* (35% of dissimilarity explained), a 3-fold increase in the prevalence of *Alisma subcordata* (27%), and the occurrence of two unique forbs—*Sagittaria latifolia* and *Cerastium vulgatum* (14%).

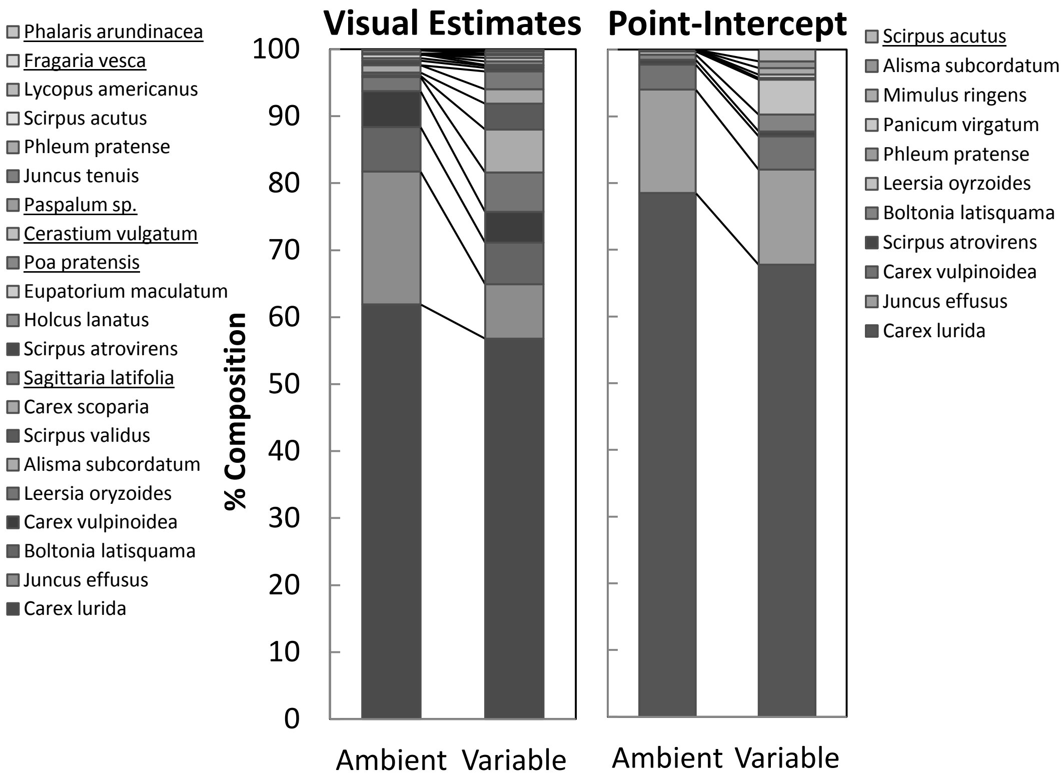


Figure 4.4. Community composition was recorded via visual estimates of % cover, and by the point intercepts method. These data represent within-treatment mean contributions to total cover and biomass respectively. Underlined species only occurred in the stressful hydrologic regime.

The stressful hydrologic regime did not lead to significant differences in α richness at the plot-level (ambient treatments had an average of 6 species per plot (n=10), while stressful treatments had 7 (α 2-tailed t=-1.4, p=0.16). Plots followed a weak negative (though non-significant) productivity diversity relationship (Linear regression r^2=0.16, $F_{1,18}$=3.58, p=0.07). Of the 32 species recorded within the experiment, 4 graminoids and 3 forbs were unique to the stressful treatment, occurring in 1-2 replicates at 1-15% estimated cover while no species were unique to the ambient treatment. Inter-plot heterogeneity was significantly greater for the stressful hydrology treatment when compared to the ambient treatment when rare species (<15% cover) were included in dissimilarity calculations (permutation dispersion : $F_{1,18}$=4.71, p=0.045 for estimated cover, $F_{1,18}$=3.15, p=0.08 for point-intercept)(Figure 4.5). Dissimilarities were greater, but not significant for the stressful treatment when rare species were not included (permutation dispersion : $F_{1,19}$=3.15, p=0.081 for the point-intercept method).

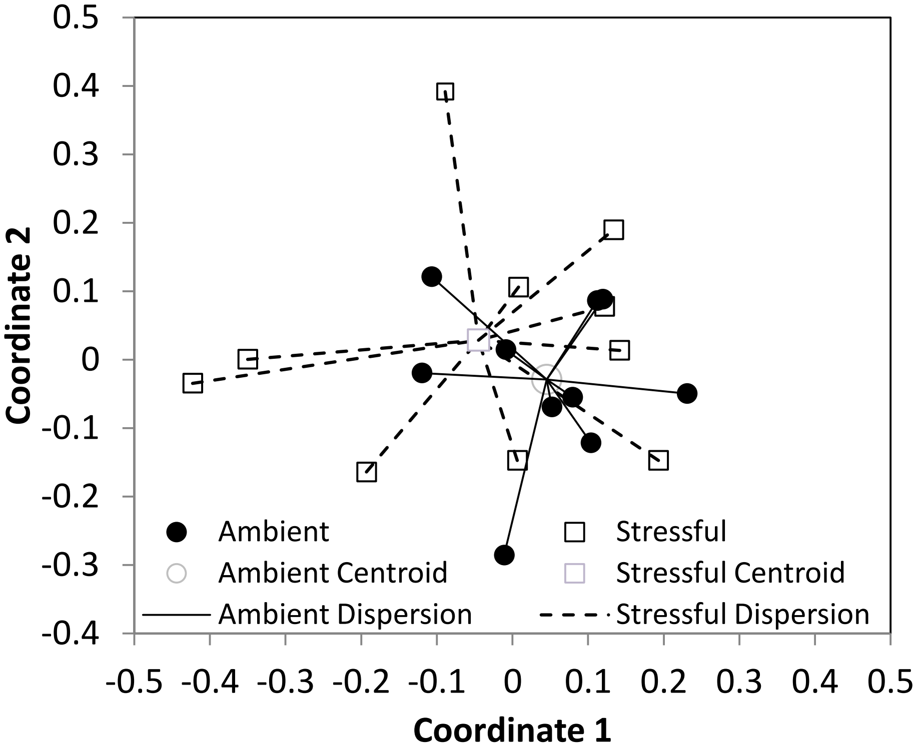


Figure 4.5. Non-metric Multidimensional Scaling of the relative abundance matrix based on visual estimates (May 2012). Multivariate distances were calculated using Bray-Curtis dissimilarity coefficients and lines represent dispersion of plot values from treatment means (large grey symbols).

Variances in mean aggregated functional trait values were significantly higher for the stressful treatment for Specific Leaf Area, Leaf Dry Matter Content, and number of seed per culm (Table 4.1). Alpha diversity did not differ significantly between treatments and species unique to the stressful treatment did not differ significantly in means or ranges of trait values from the group of species found in both treatments (data not shown). This observed increase in mean trait variance reflects the same compositional variability demonstrated via the above permutation tests for community dispersion.

Community-aggregated specific leaf area increased significantly for the stressful treatment under the visual estimation method, but not the point-intercept method, likely owing to an increased emphasis on variation in the composition of subcanopy species. The occurrence of unique species in the stressful hydrologic regime was responsible for significant heteroscedasticity in weighted averages of specific leaf area, # of seed and leaf dry matter content, as these differences were no longer significant when unique species were removed from the analysis.

Table 4.1. Results of significance tests for abundance-weighted functional trait variances and means. Amb and Stress indicate ambient and stressful treatments respectively, with the larger values highlighted in grey. Vis and P-I indicate the Visual Estimation and Point-intercept methods. Standard Deviations and Levene's test results are reported under the Variance column for abundance-weighted specific leaf area (SLA), canopy height, number of seeds per culm, leaf dry matter content (LDMC) and seed mass. Welch's test statistics are reported for mean comparisons where Levene's test results were significant. (*** = p<0.01, **= p<0.05, *=p<0.1, ns= not significant)

		Variance				**Mean**			
		Amb	**Stress**	**F**	**P**	**Amb**	**Stress**	**F**	**P**
SLA (mm^2/mg)	**Vis**	0.82	1.92	5.9	0.026^{**}	19.34	21.46	10.3	0.008^{***}
	P-I	0.48	1.71	4	0.06^{*}	18.74	19.61	2.39	0.15^{ns}

Table 4.1. (cont.) Results of significance tests for abundance-weighted functional trait variances and means. Amb and Stress indicate ambient and stressful treatments respectively, with the larger values highlighted in grey. Vis and P-I indicate the Visual Estimation and Point-intercept methods. Standard Deviations and Levene's test results are reported under the Variance column for abundance-weighted specific leaf area (SLA), canopy height, number of seeds per culm, leaf dry matter content (LDMC) and seed mass. Welch's test statistics are reported for mean comparisons where Levene's test results were significant. (*** = p<0.01, **= p<0.05, *=p<0.1, ns= not significant)

		Variance				**Mean**			
		Amb	**Stress**	**F**	**P**	**Amb**	**Stress**	**F**	**P**
Height (m)	**Vis**	0.15	0.11	0.42	0.52^{ns}	0.73	0.81	1.78	0.2^{ns}
	P-I	0.04	0.17	5.92	0.0256**	0.62	0.72	2.66	0.13^{ns}
Seed # (1000s)	**Vis**	22.1	56	14.1	0.002***	85.5	86	0	0.98^{ns}
	P-I	28.2	63.2	4.37	0.0509*	39.6	65.8	1.43	0.25^{ns}
LDMC (mg/g)	**Vis**	7.2	27.9	28.4	<0.001***	295.2	276.2	4.33	0.06*
	P-I	5	22.9	7.3	0.015**	305.1	294.4	2.1	0.18^{ns}
Seed Mass (mg)	**Vis**	0.16	0.23	0.39	0.54^{ns}	0.82	0.99	3.57	0.08*
	P-I	0.17	0.15	0.04	0.85^{ns}	0.95	0.94	0.03	0.87^{ns}

Discussion

The imposed stressful hydrologic regime yielded increases in amplitude (100%) and frequency (36%) of water table fluctuations consistent with the direction of projected shifts for Midwestern wetlands (Wuebbles & Hayhoe 2004; USGCRP 2009). These had detectable effects on artificial wetland communities, particularly the composition of low-abundance species, and the value and variability of community-aggregated functional traits.

Though significant, RVI differences reflected non-treatment differences among plots during establishment that were not explained by soil volume, water table depth or drainage rates.   As treatments did not differ significantly in accumulated biomass, treatment associations with productivity will be considered cautiously.

As declines in RVI reflect unexplained non-treatment effects, productivity will be interpreted as an independent source of variation from treatment effects (where possible). Plots within the stressful hydrologic regime treatment accumulated biomass slower than ambient plots as evidenced by differences in the RVI index in the spring (Figure 4.3). Contrasts in plot-level RVI can arise from differences in canopy density (i.e. differences in the vegetation/background ratio), or canopy quality (i.e. the amount of functional mesophyll and/or chlorophyll in the visible canopy)(Jackson & Huete 1991). The declines in RVI observed here coincided with the period of progressive canopy closure in the spring. The intersection of RVI means in June suggests that canopies reached a similar maximum potential productivity but took longer to close in mesocosms that would be subjected to the stressful hydrologic regime. The lack of differences in RVI in the mid-late growing season (coincident with experimental manipulations) suggest that the stressful hydrology treatment was insufficient to cause discernible declines in productivity in the late season when differences in canopy quality were no longer obscured by differences in density. RVI means for the period of active growth were strongly correlated with peak biomass observed in October 2012 (Figure 4.3), lending support to the idea put forth by Chaves and Pereira (Chaves & Pereira 1992) that accumulated biomass can be approximated via measures of photosynthetic rate and foliar area.

Two protocols were used to estimate community composition and structure. Visual estimates were incorporated to consider all species present (Greig-Smith 1983) while the point-intercept method (Jonasson 1988) was modified to assess canopy components. The two methods were in general agreement when considering the relative composition of species forming the canopy (Figure 4.4), but the point-intercept sampling regime was not suitable for describing community differences below the canopy, especially for low-abundance species. As a result, community differences discussed here refer to the results of the visual estimation method unless otherwise indicated.

Compositional differences arose primarily from subordinate species, where the stressful hydrologic regime yielded an increase in forb prevalence and a shift in forb composition. Forb prevalence increased by 25% in the stressful treatment, which was largely the result of increasing abundance of two obligate hydrophytes (*Alisma subcordata* and *Sagittaria latifolia*). Compositional differences were partially determined by a decrease in *Boltonia latisquama*, a facultative wetland species. These results indicate that the stressful hydrologic regime yielded sufficient intensity and duration of flooding to restructure the forb fraction of these communities by selecting species with a higher inundation tolerance.

The stressful hydrologic regime yielded plots that were compositionally less similar than those in the control treatment. A large body of literature has considered the implications of patch-similarity in communities in the form of species compositions and of traits (Weiher & Keddy 1995; Weiher et al. 1998; Fukami & Lee 2006; Schamp et al. 2008). At the local scale, patches are often predicted to be more similar where either biotic or abiotic adversity is maximized, limiting the number of species that can persist (Keddy 1990). Intermediate conditions represent a relaxation in the potential biotic and environmental constraints on community assembly, and patches tend to vary in composition as a function of history and stochastic processes (Grime 1979). This experiment addressed differences in assembly at the local scale (a single habitat) as conditions and the species pool were more homogenous than under natural conditions. An increase in community dispersion paired with a decrease in productivity suggests the stressful hydrologic regime saw a decrease in the importance of biotic adversity (competition) in structuring these communities (Weiher & Keddy 1995; Grime 2001) leading to a greater importance of stochastic processes in determining the communities present.

Functional traits differed between treatments in both their variability and community aggregated means. Increasing trait heterogeneity in the stressful treatment was largely the result of an increase in β diversity which involved the arrival of 5 colonists from outside the experimental mesocosms and 2 seeded species (*Sagittaria latifolia* and *Scirpus acutus*) representing an increased breadth of variation in observed traits. Only SLA differed significantly between treatments in community-aggregated means. This could be the result of differences in stress-disturbance regime experienced by seedlings as compared to adult plants (Grime et al. 1988; Grime & Hillier 1992) as the majority of plot compositional differences were in the understory. Flooding amplitude and frequency may have a more severe effect on seedlings and small plants as they would have narrower optimal water table ranges than larger ones. Alternatively, guild structure may have contributed to the observed difference as forbs were more prevalent in the stressful hydrology treatment and guild-aggregated forb SLA was 65% higher than that of graminoids.

This study has implications both for native community formation and restructuring under an altered climate, and for restoration of mineral soil wetlands where seed composition and hydrology are considered. The establishment of communities under a static water table followed by a more natural variation in hydrology yielded a community dominated by sedges and rushes, species characteristic of moderate flooding stress. Increasing hydrologic variability led to increases in community heterogeneity which may translate to patch-scale heterogeneity of managed wetland landscapes. This patch heterogeneity provides an opportunity to augment plot-level diversity. However, it also produces a habitat where resource availability shifts dynamically in both space and time, and where colonization ability plays a stronger role in community structure, possibly making communities more susceptible to invasion.

Acknowledgements

I would like to thank the University of Akron Field Station for providing resources and space for this experiment, and Dr. Bill Mitsch and Dr. Li Zhang for critical advice on experimental infrastructure. I would also like to thank the University of Akron Department of Biology and Department of Geography and Planning for critical resources and equipment.

CHAPTER V

FORECASTING CLIMATE CHANGE IMPACTS ON THE DISTRIBUTION OF WETLAND HABITAT IN THE MIDWESTERN UNITED STATES

Abstract

Shifting precipitation patterns brought on by climate change threaten to alter the current distribution of wetlands. I developed a set of models to understand the role climate plays in determining wetland formation on a landscape scale and to forecast changes in wetland distribution for the Midwestern United States. These inferential (linear) and predictive (artificial neural networks) models combined 35 climate variables with 21 geographic and anthropogenic fixed factors for the Midwestern region of the United States. All models successfully predicted a majority of the variation in current wetland area within the Midwest and wetland area was significantly associated with climate, even when controlling for geographical arrangement and landscape context. Linear models identified a consistent negative association between wetland area and isothermality. This is likely the result of regular inundation in areas where precipitation accumulates as snow, then melts faster than drainage capacity. Moisture index seasonality was identified as a key factor distinguishing between emergent and forested wetland types where forested wetland area at the landscape scale is associated with a greater seasonal variation in water table depth. The most reliable models predicted an

increase in potential wetland area in the coming century, with areas conducive to forested wetland formation expanding more rapidly than that of emergent wetlands. Local cluster analyses identified Iowa and Northeastern Missouri as areas of anticipated wetland expansion, indicating both a risk to production within the Midwest Corn Belt and an opportunity for wetland conservation, while Northern Minnesota and Michigan are potentially at risk of wetland losses under a future climate.

Introduction

Wetlands play an important role in mitigating the impacts of flooding on a landscape scale (Hey & Philippi 1995) and effective conservation requires knowing where conditions will continue to support their creation or maintenance as the climate changes. Climate change is anticipated to bring about shifts in the pattern and timing of rainfall for the Midwestern US, yielding increases in the frequency and intensity of severe storms during the growing season and an increase in seasonal flooding from snowmelt (Wuebbles & Hayhoe 2004; USGCRP 2009). Wetlands generally act as buffers to severe flooding by diverting and retaining floodwaters (Farber 1987; De Laney 1995) but a majority of these habitats have been degraded within the conterminous United States where an estimated 59% of freshwater wetlands were filled, dredged, or otherwise altered within the last 200 years (Bedford 1999; Bridgham et al. 2006). Economic impacts of flooding have risen over the past century, not only as a function of increasing development and infrastructure along waterways and coastlines, but because of a decline in buffering capacity afforded by wetland ecosystems (Hey & Philippi 1995). Climate change has the potential to reorganize wetland prevalence, threatening what buffering capacity remains in a time when flooding is anticipated to become more frequent and severe (Farber 1987).

Wetlands respond rapidly and dynamically to shifts in hydrology (Keddy 2002), a property that is controlled by climate at both regional and landscape scales (Erwin 2009). The boundaries of lacustrine wetlands shift with lake water levels, which are intricately connected to precipitation and temperature via recharge and evaporation rates (Keddy & Reznicek 1986; Mortsch 1998; van der Valk 2005). Coastal wetlands respond dynamically to flooding and sediment accretion from tidal processes, tropical storms and river discharge (Poff et al. 2002; Nicholls 2004). Blanket bogs form as a function of precipitation and temperature with very little hydrologic connectivity to the surrounding landscape. As a result, fossils from these communities are considered to be accurate climate proxies (Barber et al. 1994; Mauquoy et al. 2002). Riverine wetlands retain floodwaters or form in oxbows where flooding deposits fresh sediment (Keddy 2002).

The wetland-climate connection is fairly direct for some habitat types (ombrotrophic bogs) but often subject to innumerable landscape and local influences (Burkett & Kusler 2000) making it difficult to predict how any particular wetland will respond to a changing climate. This leaves managers with unclear conservation targets, especially when climate forecasts predict many historic norms to be untenable in the near future (Harris et al. 2006; Zedler et al. 2012).

One solution to improve conservation targets lies in leveraging the wealth of information about the current distribution of wetlands and climate. Fine-scale geographically-explicit datasets are available that quantify both the distribution of wetlands and many of the major drivers of wetland ecosystem formation. The USGS National Wetland Inventory provides geographic extents for wetlands of multiple classifications (USFWS 2001). Drainage networks, elevation (USGS 2005a; USGS 2012) and climate models (Kriticos et al. 2012) have the potential to map long-term hydrologic variation. On the ground and remotely-sensed data shed light on land cover types, and the degree of anthropogenic disturbance. Paired with fine-scale applications of global circulation models (Kriticos et al. 2012), these data provide the opportunity to predict shifts in the broad scale distribution of wetland types under future climates. Forecasted wetland distributions may be used to focus conservation efforts on developing or maintaining wetlands where the climate is projected to support their increase, and consequently, where they will be most needed to mitigate flooding.

I developed a system of geographically explicit models to evaluate the connection between climate and the distribution of two major wetland types (emergent and forested). The emergent versus forested dichotomy represents one of the broadest-scale distinctions between wetland vegetation types and these models represent the beginning of a process to further resolve wetland compositional differences on a landscape scale. Wetland type is primarily determined by the frequency and severity of flooding (Keddy 2002). Emergent wetland communities are resilient to or even require frequent or persistent floods that occlude more competitive upland species (Keddy 2002). Forested wetlands are characterized by low-frequency flooding, as woody species are generally less tolerant of prolonged inundation than herbaceous species (Toner & Keddy 1997; De Jager & Thomsen 2012; Deng et al. 2013). These ecosystems host fundamentally different communities and yield different goods and services (Weisberg et al. 2013).

In this study, I tested the hypothesis that wetland distribution remains associated with climate on a regional scale despite pervasive anthropogenic modification and I explored the implications of this association for projecting wetland area into the coming century. I tested the hypothesis that modeled wetland area would increase for the Midwest when climate change scenarios were applied, as a predicted increase in flooding frequency/intensity on the regional scale would lead to net gains in wetland area. Finally, I explored the geographic distribution of forecasted changes in wetland area and I discuss the implications of such a model as a management tool for the region.

Study Area and Datasets

The study area comprised the majority of the Midwest (as defined by the USGCRP (2009) where wetland distributions were recorded by the USFWS National Wetland Inventory (NWI) (2001). The inclusive study area comprises 960,000 km^2, 6.9% of which was classified as Forested or Shrub dominated wetlands and 1.9% as emergent marsh by the USFWS NWI. Freshwater ponds, lakes and rivers, though considered wetlands by the NWI, were not included as response variables in the model described herein.

Materials & Methods

Datasets

Shapefiles from the NWI (USFWS (2001) were compiled into a single geodatabase for the US States included in the study area. The NWI contains polygons designating the boundaries of wetlands throughout most US Counties and provides broad and specific classifications. Broad classifications include Forested/Scrub-Shrub, Freshwater Emergent, or Ponds and Rivers while specific classifications indicate hydrogeomorphic type, substrate, and major vegetation classes (Cowardin et al. 1979). The State of Wisconsin wetland inventory followed a modified sampling protocol (Johnston & Meysembourg 2002) and does not provide public access to the entirety of the wetland inventory for their State, and was therefore left out of the analysis (Figure 5.1).

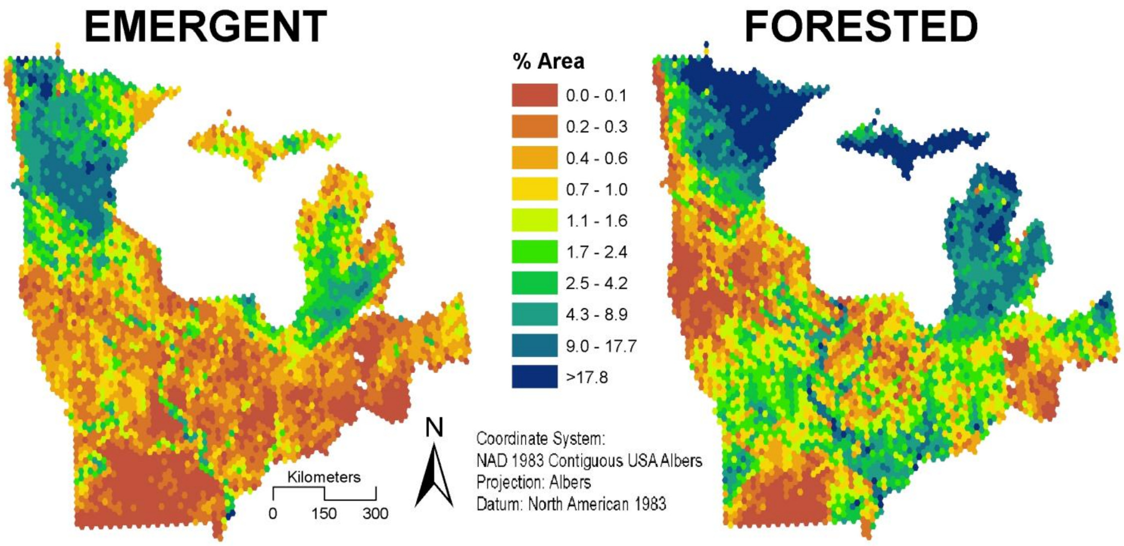


Figure 5.1. Wetlands were aggregated by type using 260km^2 hexagons (n=4307) and summarized in the above choropleths as the proportion of the area of each hexagon occupied by either emergent or forested wetlands. Color transitions between red and green represent forested wetland quantiles. The National Wetland Inventory lacks publically accessible records for Wisconsin (upper middle) and for southeastern Ohio (lower right corner) and these regions are not included in the analysis. Hexagons expressing the maximum quantiles (acreage/area) tend to be in the northern portions of the study area, or along major drainage basins. Moving northward through Minnesota and Michigan, Freshwater Emergent marshes become less prevalent as Forested wetlands increase in area.

Bioclimatic surface layers were extracted from CliMond global climate products (Kriticos et al. 2012) representing current and projected conditions based on historic climate records and two Global Circulation Models from the IPCC 4th assessment (Solomon et al. 2008). These were upscaled from the highest spatial resolution (1 km spatial resolution) climate surfaces interpolated for the major continental areas of the world (Hijmans et al. 2005), representing 35 variables that encapsulate climate metrics considered to be most relevant to biological functions (Hutchinson et al. 2009). These climate variables are nearly evenly distributed among metrics related to temperature, precipitation, solar radiation, and soil moisture (Figure 5.2).

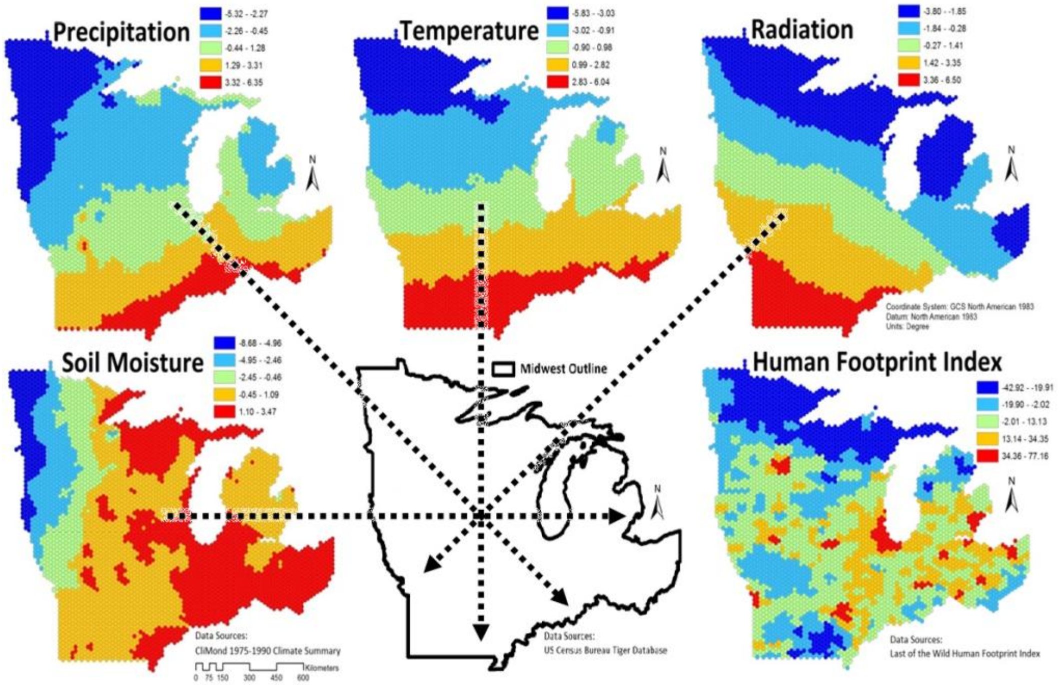


Figure 5.2. The above 5 choropleths represent the spatial distribution of PCA scores for each climate component (precipitation (8 variables, 64% variance), temperature (10,66%), radiation (8,67%), soil moisture (8,59%) and the human footprint index (6,73%) based on correlations). The majority of variance in the 4 climate components can be summarized by simple directional gradients (arrows in the central Midwest outline represent gradients along which variance in each variable class are distributed (e.g. precipitation varies along a Northwest-Southeast Gradient). All high values are coded in red for consistency.

'Current' conditions represent climate summaries for the period 1975-1990 calculated from products in the Worldclim database (Hijmans et al. 2005) that were reformatted following the procedure outlined by Kriticos et al. (Kriticos et al. 2012). Projected climate surfaces for 2100 were used (CSIRO Model for A1B and A2 emissions scenarios (Nakicenovic et al. 2000)) to develop climate differential surfaces (future conditions –

current conditions)(Appendix D.1) and to apply the model described below to predict wetland compositional shifts throughout the study area.

A series of additional pertinent datasets were also included in the model to quantify their relative impact on wetland area and to control for their effects when projecting future wetland distributions under different climate scenarios. National Land Cover classes (200m resolution) were clipped from the 1992 database (USGS 2005b) and included as candidate model variables to account for contextual variations in upland habitats summarized at the regional level (Table 5.1).

Table 5.1. Percent coverage by land cover class for the Midwest (USGS 2002). Classes are sorted in order of largest to smallest areal coverage.

Land Cover Type	% Area
Dryland Cropland and Pasture	38.43
Cropland/Woodland Mosaic	17.98
Cropland/Grassland Mosaic	15.45
Deciduous Broadleaf Forest	13.57
Mixed Forest	10.09
Urban and Built-Up Land	1.45
Water Bodies	1.39
Evergreen Needleleaf Forest	0.76
Savanna	0.54
Grassland	0.30
Irrigated Cropland and Pasture	0.04

The Global Human Footprint Index (Sanderson et al. 2002; WCS & CIESIN 2005) was also included to quantify the degree of landscape-level habitat alteration directly related to anthropogenic factors (Figure 5.2). The Human Footprint Index indicates areas of human influence on ecosystems by combining anthropogenic land-cover types with human population, nighttime lighting, and transportation networks. Finally, components of elevation were summarized from the National Elevation Dataset (100m resolution)(USGS 2012) to describe topographic variability and landscape position of each sampling unit.

Compatibility and Data Processing

All metrics were summarized using a grid of 260km^2 hexagons distributed over the 960,000km^2 study area (n=3638). This method provided a consistent means of summarizing the above datasets using coincident points and it represents a compromise among the spatial scales at which the component metrics vary. A hexagonal grid was used rather than the traditional square tiled grid to optimize visualization of connective elements at the landscape scale. As many wetlands in the sample area follow linear features (streams, rivers, and pond fringes) the hexagonal grid was deemed a more appropriate technique for preserving these spatial relationships (Birch et al. 2007). The 260km^2 hexagonal grid represents an upscaling of all component metrics to varying degrees based on the input data scale. All upscaling was performed after first projecting shapefiles (or rasters in the case of climate surfaces) using US Contiguous Albers Equal

Area Conic projection. Wetland inventory data were summarized (upscaled) as the cumulative percent total acreage of each broad wetland class for each hexagonal sampling unit. Climate data (originally at 10’ resolution) were standardized by averaging values for the inclusive area within hexagons. Proportional area for each land cover class was recorded for hexagons as a measure of landscape-level coverage type and mean and coefficient of variation for the Human Footprint Index (originally 1km resolution) were calculated. Finally, the distance to the nearest persistent river or coastline was calculated for each hexagon as a measure of broad-scale connectivity to these hydrography networks. Rather than including all possible stream classes, which would overlap all hexagons, only major rivers were included as defined by the US National Hydrography Dataset (Simley & Carsell Jr. 2009). All hexagons that intersected a major river or a shoreline of one or more of the Great Lakes received a score of 0 for this metric.

Model Development

Predictor and response metrics were first compiled into a single geodatabase. Partial Mantel tests were used to determine whether the multivariate distance matrix for climate was significantly associated with that of wetland composition while controlling for space and contextual fixed factors (land cover, human footprint, distance to major rivers, and elevation). All distance matrices were generated using Bray-Curtis coefficients with the exception of location, which incorporated Euclidean coefficients.

A simple linear model incorporating all independent variables was inappropriate to make predictions due to severe predictor multi-collinearity and the variety of distributions for predictor variable classes. Artificial Neural Networks (ANN) have been proposed as a means to circumvent these issues (Zhang et al. 1998) to assess the relationships between individual predictors and responses (Lek & Guégan 1999), though using algorithms that are not easily deconstructed. As a compromise, a linear model paired with collinearity reduction techniques was used to more easily explore the strength and direction of relationships between predictor variables/classes and response variables while an ANN-based model was applied to more reliably predict future climate scenarios.

Linear Model

Linear models were developed to describe the connection between climate variation and wetland demography. Two models were constructed using all 54 independent variables (Appendix D.1) to separately predict Freshwater Emergent Wetland and Forested/Scrub-shrub percentages using the 'lm' function in R (R Core Team 2013). Forward and reverse search functions were used to minimize Akaike Information Criterion (AIC) for each of the two models using the 'scale' function in R (Hastie & Pregibon 1992; Venables & Ripley 2002; R Core Team 2013) and revised linear models were then generated using these variable subsets. Model residuals were tested for normality (Shapiro-Wilks test) and mapped to assess spatial patterns in model prediction error. Local and regional cluster analyses (Moran's I and Anselin's Moran's I) were conducted to assess the significance of spatial clustering of residuals, and identify localities with non-normal residual distributions). In order to reduce multicollinearity and generate variable coefficients whose signs and magnitudes could be interpreted, VIF reduction was performed by constructing a set of models while sequentially removing variables with the maximum VIF until all independent variables expressed a VIF <10 (Hair Jr. et al. 1992). T-statistics were generated for each independent variable, assigning a magnitude, direction, and significance to each predictor-response pair.

Model coefficients were applied to climate projections for the year 2100 under the A2 SRES while holding all remaining factors constant. Model predictions for the current wetland distribution were subtracted from the 2100 projections to yield projected differences in wetland area. These differences were mapped to assess patterns in climate leveraging and cluster analyses were performed to delineate regions where wetland area is predicted to expand or contract.

Artificial Neural Network (ANN)

I constructed an Artificial Neural Network using the inclusive set of predictor variables derived from the AIC reduction technique applied for the linear models to predict the magnitude and spatial variation in future wetland area in the Midwestern United States. Artificial Neural Networks are used primarily for pattern recognition in complex datasets where there are many predictor variables (Cheng & Titterington 1994). The core topology of the Artificial Neural Network (hereafter called ANN Model, or simply ANN) consisted of a single layer of 6 hidden nodes calculated using the hyperbolic tangent activation function (Zhang et al. 1998). Multi-layer topologies did not perform appreciably better than a single-layer network, and these approaches were discarded in favor of the simplest model architecture. Gradient boosting was applied (n=7 iterations yielding a total of 42 hidden nodes) to improve forecasting accuracy (Friedman 2001) and the learning rate was set at 0.1 to reduce the likelihood of over-fitting. A weighted decay function was incorporated into the model, as this approach is recommended to improve model performance and avoid over-fitting when importance varies among predictor variables (SAS Institute Inc. 2012). Model training was performed using 67% of the dataset, where the remaining data constituted a random holdback for model validation. Residual means were tested for significant deviation from zero (t-tests), as network construction does not constrain residuals to zero and directional bias in mean residuals can affect forecasting accuracy (Hyndman & Athanasopoulos 2013). Diagnostic tests of the model residuals were performed as described for the linear models (above). Model coefficients were applied to climate projections for the year 2100 under the A2 SRES while holding all remaining factors constant.

This predictive framework isolates the modeled effects of climate on projected wetland area, but it is unrealistic to expect the constituent covariates to remain static. United Nations estimates project a 62% increase in the US population from the year 2000 to 2100 (United Nations 2012). It is reasonable to assume that this will lead to an increase in the intensity of land use and human impact even if stringent sustainability measures and green technologies are implemented. In addition to the projections described above, the ANN model was applied to model projections for 2100 that, in addition to climate A2 climate projections, incorporated a 25% increase in the human footprint index and a 62% increases in Urban and Dry Cropland (LCVR1 and LCVR2) cover classes (with concomitant and uniform decreases in remaining land cover classes so that land cover totals were constrained at 100%).

Though analyses were primarily focused on the 2100 projected climate for the A2 model, the ANN model was also applied to the A1B SRES for comparison of the projected % change in wetland distributions for 2100.

Results

A Partial Mantel Test (Smouse et al. 1986) indicated that the (3638X3638) distance matrices generated for climate (35 variables) and wetland acreage (Forested vs Emergent) were significantly associated (Mantel r=0.17, p=0.001, based on 999 permutations) when controlling for geographic distance among hexagon centers. A second Partial Mantel Test indicated that the distance matrix for wetland acreage (Forested vs Emergent) was significantly associated with climate (35 variables) when controlling for an additional distance matrix comprising contextual fixed factors including geographic distance, land use, land cover, elevation, and distance to major tributaries)(Mantel r=0.17, p=0.001, based on 999 permutations).

The simultaneous forward and reverse step function successfully reduced AIC and the predictor dataset from 56 to 40 variables for emergent and 33 variables for forested wetlands. The resulting linear models were highly significant (Emergent

$F_{39,3598}$=128.3,p<0.0001, Forested $F_{32,3605}$=320.7,p<0.0001), encapsulating a majority of the variation in wetland area for both habitat types at the 260km^2 scale (Emergent R^2=0.58, Forested R^2=0.74). These models still incorporated variables with unacceptably high VIF scores (>10), indicating that though useful for prediction, individual variable coefficients are not interpretable (Appendix D.2). Sequential variable removal for VIF reduction further limited the number of predictor variables to 19 for Emergent and 17 for Forested wetlands (Emergent R^2=0.47, Forested R^2=0.57)(Table 5.2).

Table 5.2. Linear model coefficients and significance following variable reduction to minimize AIC and to restrict all variables to VIF scores <10. *Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '*

	Emergent					Forested				
Variable	Est	StErr	t	VIF	Sig.	Est	StErr	t	VIF	Sig.
(Intercept)	14	0.7	21.3	NA	***	6.4	1.1	5.8	NA	***
XCoord						0	0	-0.5	7.3	
ELEVMN	0	0	-3.4	3.2	***					
ELEVMIN						0	0	1.9	2.7	.
ELEVSTD	0	0	-7.4	1.5	***	0	0	-10.1	1.5	***
LCVR1	0.7	0.1	5	1.1	***	-3	0.3	-10.9	1.2	***
LCVR2						-2.9	0.1	-30.9	5.4	***
LCVR5	0.5	0.1	9.6	1.3	***	-2	0.1	-15.5	2.1	***
LCVR6	0.6	0	14.5	1.5	***	-2	0.1	-19.5	2.8	***
LCVR10	-0.7	0.4	-1.8	1.2	.					
LCVR11	0.4	0	7.6	2.8	***	-2.2	0.1	-17.9	4.5	***
LCVR15	0.1	0.1	2.2	1.8	*					
MAXhuman	0	0	-7.8	2.4	***	0	0	1.6	2.4	
STDhuman	0	0	5.5	2.1	***	0	0	-4.9	2.2	***
bio3	-10.3	1	-10.7	7.6	***	-28.1	1.7	-16.8	6.3	***
bio8	-0.1	0	-5.8	5.2	***	-0.2	0	-13.7	2.6	***
bio13	0	0	5.2	4.2	***	0	0	2.5	5.7	*
bio24	0	0	8.4	5.7	***					
bio25	0	0	2	2.7	*	0	0	-5.5	2.5	***
bio26	0	0	-12	4.8	***					
bio30	-3.7	0.2	-16.2	3.5	***					
bio31	-3.9	0.5	-8	7.5	***	13.5	1	14.2	7.9	***
bio34						6.2	0.4	15.5	2.4	***

The linear model identified a negative association between wetland area and isothermality that was highly significant ($p<0.0001$) and independent of wetland type (Table 5.2). Moisture index seasonality was identified as a key factor (based on coefficient magnitudes) distinguishing between emergent and forested wetland types where high values were associated with forested wetlands and low values were associated with emergent wetlands (Table 5.2).

The ANN model produced an overall generalized $R^2=0.96$, predicting a majority of the variability in emergent ($R^2=0.72$) and forested ($R^2=0.84$) wetland areas. The reported R^2 values represent the proportion of variation explained by the model for those data not included in the training set. Model projections incorporating increases in human footprint and land cover change did not differ significantly from those of the A2 Scenario (Emergent $t=-1.25, p=0.2$, Forested $t=1.48, p=0.1$)(not shown).

Residuals for the linear model differed significantly from zero ($\bar{x}_{emergent}=0.6$, $t=13.5$, $p<0.001$, $\bar{x}_{Forested}=-2.4.$, $t=-17$, $p<0.001$) indicating an over-estimation of forested wetland area. Mean residuals for the Artificial Neural Network also differed significantly from zero ($\bar{x}_{emergent}=-0.15$, $t=-4.3$, $p<0.001$, $\bar{x}_{Forested}=-0.42$, $t=-5.2$, $p<0.001$), but the effect size of the model bias was considerably smaller (<0.5%). Residual frequency distributions were all significantly non-normal (Shapiro-Wilk $p<0.001$) though the sample size ($n=3638$) was sufficiently large to make normality testing over-sensitive (Figure 5.3).

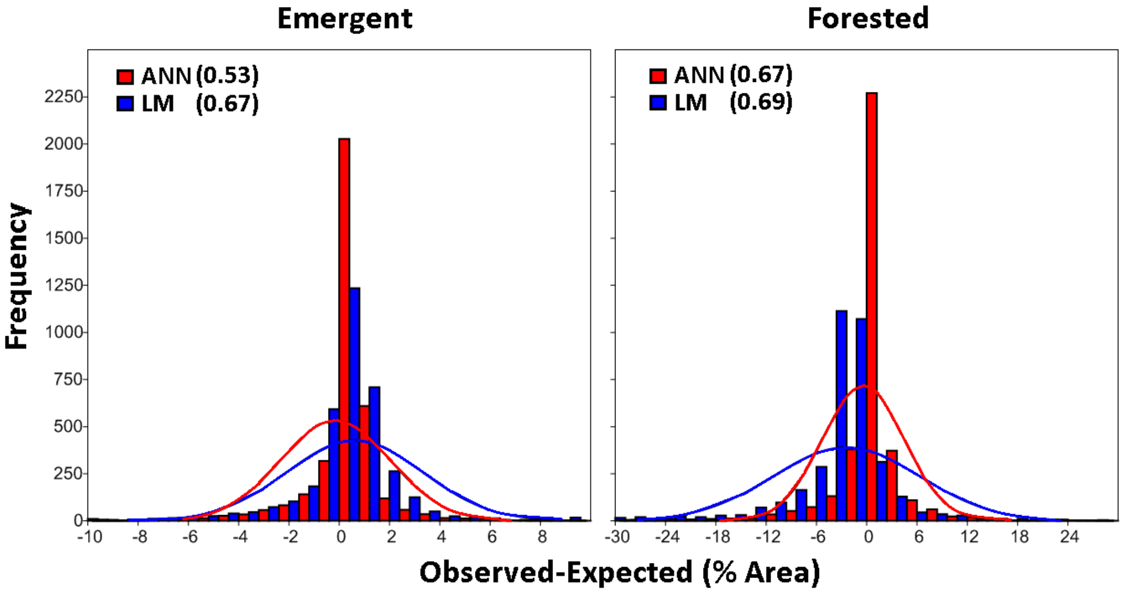


Figure 5.3. Model residual distributions. ANN model (red) and Linear model (blue) residual distributions (n=3638). Lines represent approximate fits for the normal distribution. Values in parentheses are Shapiro-Wilks W statistics for each distribution.

Model residuals were significantly spatially clustered (p<0.0001), indicating regions of model over/under-estimation (Figure 5.4). The most striking and consistent model under-estimations were for areas with atypically high proportions of wetlands. These included the Mississippi river, northern Minnesota and central Michigan where the abundance of surface water from tributaries and lakes likely contributed to an increase in wetland area that was uncharacterized by the model variables.

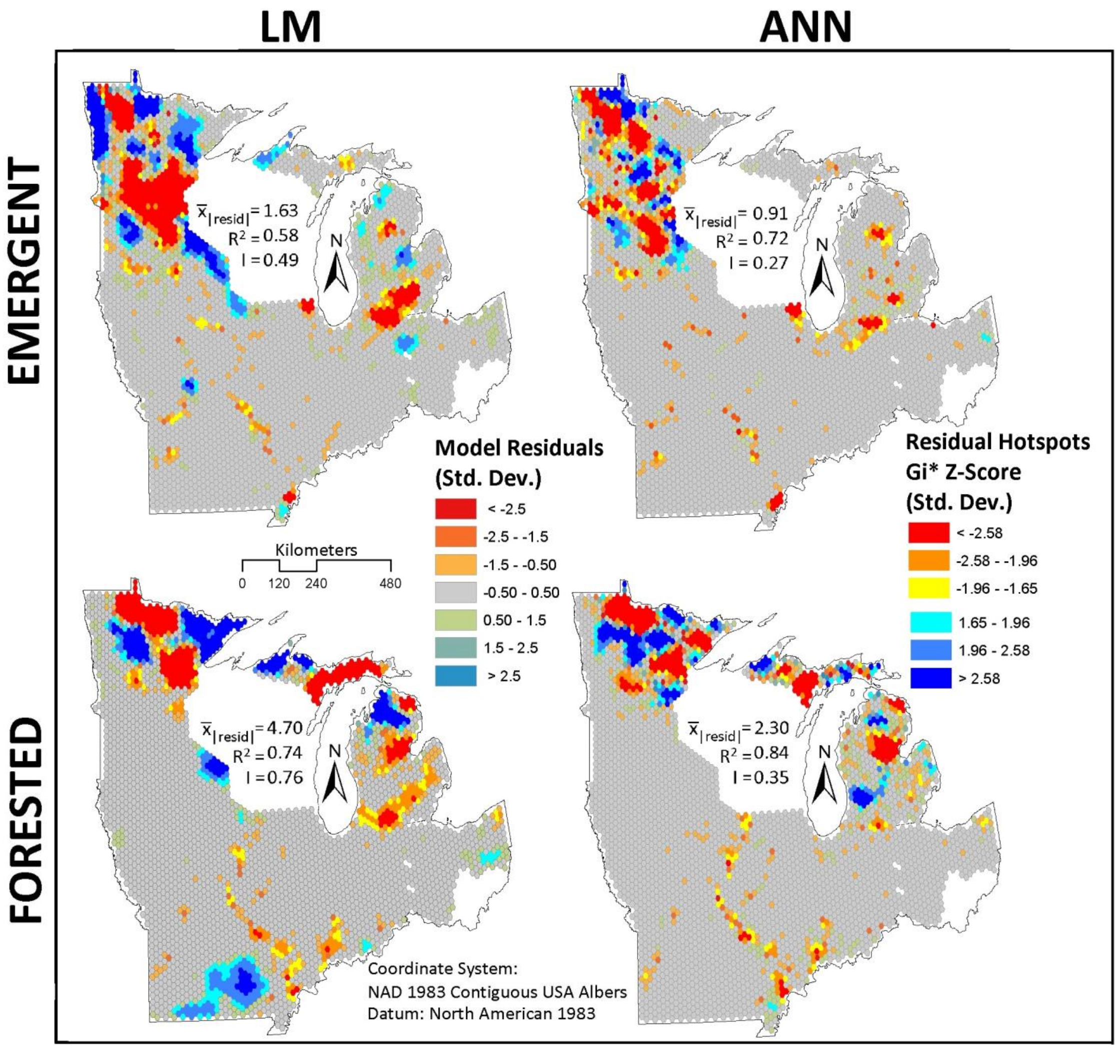
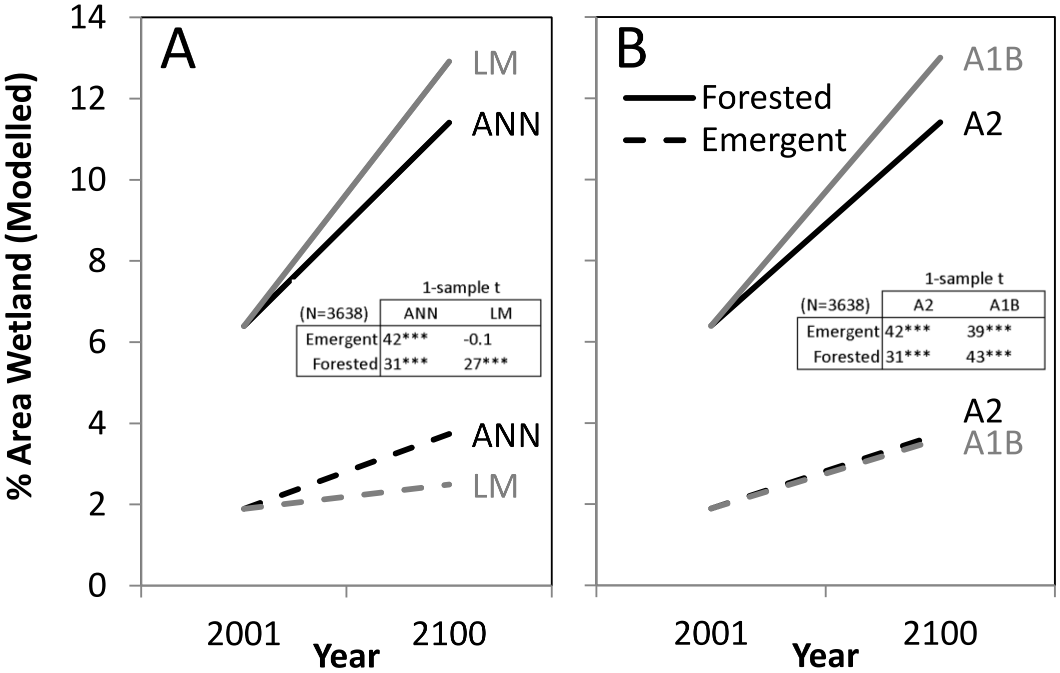


Figure 5.4. Model residuals for linear models (LM)(Left) and the constructed Artificial Neural Network (ANN)(right) for both Emergent (top) and Forested (bottom) wetland habitat types. $\bar{x}_{|resid|}$ indicates the average deviation of model predictions from observed values. Reported R^2 values represent the proportion of variation in 2001 wetland areas explained by each model. Moran's I values are reported for global cluster analyses. Clustering of low and high values are mapped using z-scores calculated for the Getis-Ord Gi* statistic. Significant low value clustering (red/orange) indicates model under-estimation of current wetland area while significant high value clustering (light blue) indicates model over-estimation.

With the exception of linear model projections for emergent wetland area (1-sample t=-0.09, p=0.9), all models forecasted significant increases in area conducive to emergent and forested wetland formation for the year 2100 (Figure 5.5). Projected forested wetland area was 3.5% greater for the linear model than that of the ANN model, while the ANN model alone forecasted a 2% increase in emergent wetland area (t=9.3, p<0.0001)(Figure 5.5A). The ANN model forecasted significant increases in both emergent and forested wetland area for the year 2100 under the A2 and A1B SRES (1-sample t-test, p<0.0001)(Figure 5.5B). The A1B Emissions Scenario (Nakicenovic et al. 2000) yielded significantly greater increases in wetland area when compared to the A2 SRES for forested, but not emergent wetlands ($t_{Forested}$=6.6, p<0.0001, $t_{Emergent}$=1.87, p=0.06)(Figure 5.5B).



1-sample t

(N=3638)	ANN	LM
Emergent	42***	-0.1
Forested	31***	27***

1-sample t

(N=3638)	A2	A1B
Emergent	42***	39***
Forested	31***	43***

Figure 5.5. Wetland % area forecasts for the year 2100. Linear and ANN model projections of the proportion forested (solid lines) and emergent (hashed lines) wetlands for the entire study area. (A) Presents linear model (LM) and artificial neural network (ANN) projections for the CSIRO model of the A2 emissions scenario for the year 2100. (B) Presents a

comparison of ANN model projections for the A2 and A1B emissions scenarios. The table insets include 1-sample t values for the difference between current and projected wetland areas. ‘***’ Indicates significance at the $p<0.0001$ level).

Model projections for 2100 (A2 model) were significantly spatially clustered (Moran’s I $p<0.001$)(Figure 5.6) yielding increases in conditions conducive to wetland formation throughout the majority of the study area. Qualitatively, projected wetland area differences fell along a latitudinal gradient for the ANN model, with wetland losses occurring in the northernmost portions of the study area, and wetland gains occurring primarily in the southwest. The linear model was less favorable for prediction than the ANN model (owing to a greater dispersion of residuals and reduced percentage variance explained) and appears to be more sensitive to spatial boundaries in under-sampled regions of the study area (e.g. along the edges of the Wisconsin void and Michigan’s upper peninsula). However, the linear model predictions were consistent with that of the ANN model with respect to Northern Missouri and Iowa where the ANN model projected increases in both Forested and Emergent wetland area.

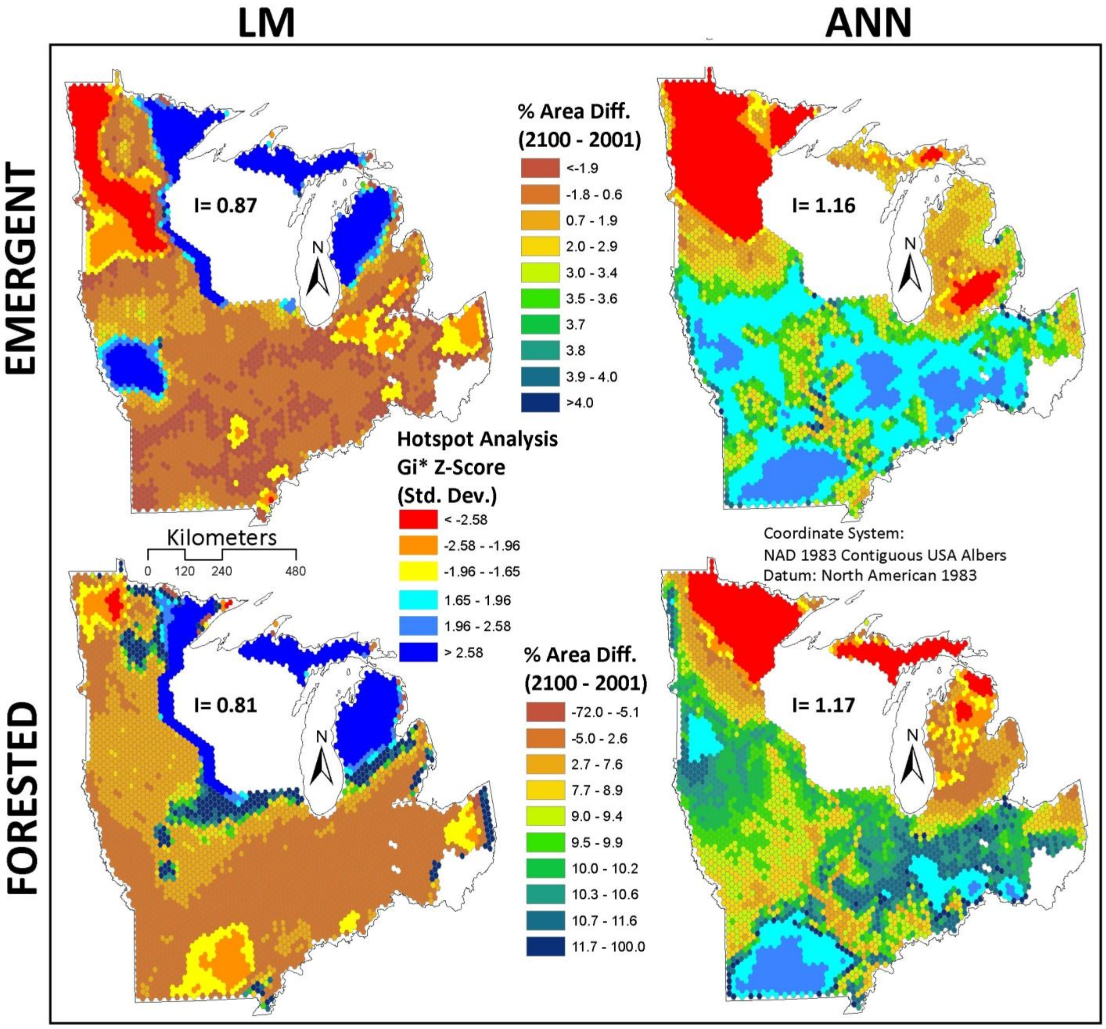


Figure 5.6. Wetland area differences for 2100 based on Worldclim CSIRO model of the A2 emissions scenario (brown-deep blue enclosed within hexagons). The Linear Model (LM)(Left) and the constructed Artificial Neural Network (ANN)(right) are reported for both Emergent (top) and Forested (bottom) wetland types. Clustering of low and high differentials are mapped using z-scores calculated for the Getis-Ord Gi* statistic. Significant low value clustering (red/orange) indicates forecasted declines in wetland area while significant high value clustering (light blue) indicates future conditions conducive to wetland area expansion. Global Moran’s I values are reported within the Wisconsin void.

Discussion

The proportion of current wetland area within the 260km^2 sampling units was significantly associated with climate, even when controlling for spatial autocorrelation and a host of regional fixed factors. This is consistent with other geographic surveys that suggest climate plays a critical role in determining wetland distribution (Erwin 2009). It also suggests that even though human activity has converted a majority of wetlands in the Midwest for other purposes (Bridgham et al. 2006), the prevalence of remaining habitat depends largely on climate and historic conditions.

As expected, the AIC-reduced linear models (though significant) did not perform favorably as inferential tools, as multicollinearity affected the signs and magnitudes of model coefficients (Appendix D.2). This precluded identifying the effect of all variables on wetland area simultaneously. The inclusive models did however generate better predictive power than VIF-reduced models, and these were used to compare predictive outcomes with those of the ANN model.

VIF-reduced models identified key variables in determining wetland area within the study region, and variables that can successfully distinguish between forested and emergent wetland variation. These models identified a negative association between wetland area and isothermality. Isothermality represents the ratio of diurnal/annual temperature ranges (Nix 1986), and represents the thermal ‘stability’ or ‘evenness’ of a region relative to annual variations in temperature (O'Donnell & Ignizio 2012). Isothermality likely affects wetland formation and maintenance indirectly by influencing seasonal hydrologic cycles. Seasonal flooding occurs as a result of spring snowmelt in portions of the study area exhibiting low isothermality (particularly Minnesota and Michigan). This diurnal instability may lead to an increasing rate of snowmelt in the spring, while increases in winter precipitation will produce larger daily runoff totals. Consequently, decreasing isothermality works in tandem with increasing winter precipitation to generate a more variable hydrograph with an increased frequency of soil saturation and/or inundation in northern portions of the study area.

Moisture index seasonality was identified as a key factor distinguishing between emergent and forested wetland types. Emergent wetlands were associated with water tables that were relatively constant through time (low soil moisture seasonality) while forested wetlands were associated with greater seasonal variation (high soil moisture seasonality). This model assembly reinforces the consensus that hydrology is a key determinant of wetland community composition (Mortsch 1998; Keddy 2002) and that the intensity/frequency of flooding (hydrologic variability) determines not only whether a wetland exhibits woody or herbaceous vegetation (Toner & Keddy 1997), but the relative prevalence of these habitat types on a regional scale as well.

Climate means (average temp, average total precipitation) never emerged as the best predictors of wetland area. Rather, climate extremes and measures of variability accounted for a greater proportion of variation in wetland area. This emphasizes an important and often overlooked distinction for wetland vegetation. Wetland plants are characterized by their tolerance of inundation (Menges & Waller 1983; Blom & Voesenek 1996; Blom & Voesenek 1996; Jackson & Colmer 2005; Luo et al. 2008). Inundation functions more to restrict incursion of non-wetland species than to promote wetland species per se (Mitsch et al. 2009). As a result, extremes in soil moisture likely indicate this restriction of upland species where hydrophytes are capable of persisting. Soil moisture and precipitation means may be very similar for upland and wetland areas, but measures of variability or extremes encapsulate the frequency and intensity of this important source of stress. Furthermore, this highlights an historic overemphasis on climate means as drivers of ecological change as identified by Smith (Smith 2011) and supports explicitly addressing climate variability in both experimentation and modeling (sensu (Thibault & Brown 2008)).

All models predicted an increase in wetland area for the A2 emissions scenario for the year 2100 (Nakićenović & Swart 2000). Wetlands were projected to increase in total area from 78,000 km^2 observed in 2001 to a potential coverage of 143,000 km^2 representing nearly an 83% increase in habitat conducive for wetland formation in the Midwest United States. Further application of the ANN model predicted increases in wetland area under both the A1B and A2 emissions scenarios, even when altering human impact and land cover variables to reflect increases in anthropogenic land use. Surprisingly, model projections incorporating increases in human footprint and land cover change did not differ significantly from those of the A2 scenario, indicating that the ANN Model construct did not heavily weight land cover or the human footprint index as wetland area predictors. This is likely due to the relatively pervasive land use in the region, yielding insufficient examples of un-impacted landscapes (with the possible exception of the northernmost extents of Minnesota and Michigan). The remaining patterns in wetland distribution at the 260km^2 scale likely still reflect climatic and geologic drivers despite pervasive fine-scale land cover reorganization.

Projected wetland area increases should be interpreted as increases in area conducive to wetland formation, which can alternatively be interpreted as an increased incidence of flooding or soil saturation within a predominantly agricultural landscape. A total of 38.43% of the Midwestern land surface was classified as un-irrigated cropland as of 1992 (USGS 2005b). The majority of this area is concentrated in the Corn Belt, a band stretching Northwest-Southeast which coincides with significant clusters of both forested and emergent wetland increases. This suggests, as predicted by Strzepek et al. (1999) and Rosenzweig (2002;2004), that crop production in the Corn Belt will be at an increased risk of water-logging or flooding stress under a future climate. This may be ameliorated somewhat by the concurrent predicted 175km Northeastern shift in the Corn Belt with increasing temperature (Newman 1980), but the absence of wetland distribution data for Wisconsin makes projecting wetland area for this new agricultural region suspect (at least for the model included here). Hydrologic control will become more difficult within the current Corn Belt, requiring management strategies that account for increases in soil saturation and runoff on a landscape scale. Furthermore, Missouri and Iowa may well become hotspots of wetland restoration and construction, where runoff retention becomes a much needed ecosystem service that wetland creation/expansion can provide and the climate yields conditions that make wetland creation and maintenance less costly.

The ANN models predicted declines in both emergent and forested wetland area for the Agassiz and Tamarack Basins as well of the Central Lakes Wetland Ecological Units of Minnesota (MDNR 1997) and Michigan's Upper Peninsula where some of the largest peat-accumulating and mineral soil wetland complexes are found. These areas are also the least impacted by humanity in the Midwest (Human Footprint Index=19, vs. remainder of study area=42), suggesting that, in the absence of proactive management, the most valuable wetlands in terms of habitat connectivity, biodiversity, and carbon sequestration will be exchanged for recently created wetlands in a largely fragmented agricultural landscape.

Restoration and conservation of wetlands have not traditionally made explicit considerations for a changing climate on management practices (Erwin 2009). These models, and others like them, can serve to help revise regional targets for wetland creation and mitigation, incorporating climate resiliency into plans to preserve wetland ecosystem services in the future. Moreover, wetland distribution modeling has the added benefit of identifying regions of future hydrologic instability and provides the opportunity to proactively avert losses in food production, infrastructure and human life by mitigating increasing flood severity before it is realized on a regional scale.

CHAPTER VI

CONCLUSIONS & INTEGRATION

Increases in the frequency and intensity of heat events and flooding anticipated over the next 100 years (Solomon et al. 2008) altered the stress-disturbance regime experienced by wetlands in the Midwestern United States. Shifts in productivity were associated with modulations in both community structure and community-aggregated functional traits. Considering trait shifts in terms of plant survival strategies support the notion that projected climate change will limit the occurrence of stable, high-yield wetland ecosystems in warm temperate regions. Modeling of wetland distribution within the Midwestern United States identified connections between climate and existing wetland distribution, independent of anthropogenic modulations of the landscape. This modeling approach projected increases in total wetland area for the region, most of which will be concentrated in areas of intensive agriculture. These increases in wetland area suggest that, with large-scale land management, wetland construction in the Corn Belt may greatly outweigh the costs of forfeited cropland by buffering against flooding, and serving as nutrient and carbon sinks (Mitsch et al. 2009; Mitsch et al. 2013).

Integration – moving forward

The greatest problems facing the modern world, and therefore most pressing topics of consideration for ecologists, deal with the interaction between processes at multiple scales (Turner et al. 1989; Levin 1992). The local application of synthetic fertilizers has supplemented natural inputs to nitrogen and other nutrient cycles, yielding a virtually global experiment in nutrient addition that exceeds terrestrial N-assimilation rates (Vitousek et al. 1997). Artificial chemosynthesis from the production of plastics to synthetic hormones has changed the composition of bio-active compounds pervading most of Earth’s ecosystems (Meybeck 2003). Greenhouse gas emissions have led to questions of how the entire climate system and its components will affect life on earth (Chaves & Pereira 1992; Melillo et al. 1993; McCarty 2001; Thomas 2004; Thuiller 2004; Harris et al. 2006; Williams & Jackson 2007). We are living in an age of ecological change and there is a pressing need for the ability to ‘scale up or down’ observations to understand their implications for the natural world.

Integration of field ecology with modern geographic information systems (GIS) has the potential to improve and inform traditional sampling efforts and to yield a clearer understanding of the relationships between climate and ecosystems. Ecology and geography have developed complementary tools and techniques, and have traditionally subdivided questions in terms of scale. Often, ecologists address causative relationships within systems on a local scale while geographers can address patterns of correlated relationships across space. Ecologists can manipulate systems with known inputs and infer processes on short time scales; while geographers can leverage decades of remote sensing information to infer processes over relatively longer time scales (Foster 2002). Ultimately, field ecology gives geographers the means to test proposed mechanisms governing regional patterns while geography gives ecologists the means of determining whether theory developed within restricted localities scale up to landscape, regional, and global processes. Climate change affects every level of biological and spatial organization, and comparing how these processes change or interact on different spatial, temporal and organismal scales will generate a clearer picture of how ecosystems change in the future.

This dissertation forms an integrated approach to understanding the connections between climate and the form and function of wetland communities. First, it leverages remote-sensing technology to detect changing productivity within a single growing season (a critical metric for discerning the effects of heat stress on vegetation), and uses vegetation indices developed by geographers (Jackson & Huete 1991; Delalieux et al. 2009) to detect and model productivity. Second, I use sampling regimes and spatial analytical techniques developed by geographers to improve the design of field experiments (Figure 3.1) inspired by (Snyder et al. 2005). And finally, I use geographic information systems to model the climate-wetland connection at the scale of the Midwest. Geographic information systems (GIS) represent the only avenue for evaluating processes at these spatial scales, and the inclusion of this modeling effort allowed me not only to detect effects of climate change on local productivity and composition, but to concurrently test the implications of a changing climate on the composition and distribution of wetland habitats.

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APPENDICES

APPENDIX A.1

SOURCES FOR FUNCTIONAL TRAIT VALUES REPORTED IN THE LITERATURE

	SLA		Height	Seed Mass	
Observed Species	Source	Congener	Source	Source	Congener
Agrostis stolonifera	Poorter & De Jong 1999	Agrostis tenuis	USDA 2001	USDA 2001	
Carex scoparia			USDA 2001		
Carex vulpinoidea			USDA 2001	USDA 2001	
Cirsium arvense	Poorter & De Jong 1999			Stevens 1932	
Dactylis glomerata	Poorter & De Jong 1999		USDA 2001	USDA 2001	
Dipsacus fullonum	Kazakou et al. 2006				
Erigeron annuus	Craine et al. 2001	Erigeron annuus	USDA 2001	USDA 2001	
Galium palustre	Poorter & De Jong 1999	Galium saxatile	USDA 2001	USDA 2001	
Geum laciniatum			USDA 2001	USDA 2001	
Juncus effusus	Sutton-Grier 2008		pers obs	USDA 2001	

	SLA		Height	Seed Mass	
Observed Species	Source	Congener	Source	Source	Congener
Mentha spicata			USDA 2001	Stevens 1932	Mentha canadensis
Mimulus ringens			USDA 2001	USDA 2001	
Penstemon digitalis	Craine et al. 2001	Penstemon grandiflorus	USDA 2001	USDA 2001	
Phalaris arundinacea	Ryser & Urbas 2000		USDA 2001	USDA 2001	
Poa pratensis	Meziane & Shipley 2001		USDA 2001	USDA 2001	
Polygonum hydropiperoides	Poorter & De Jong 1999	Polygonum persicaria		USDA 2001	
Scirpus cyperinus	Sutton-Grier 2008		USDA 2001	USDA 2001	
Sonchus asper				Stevens 1932	Sonchus arvensis
Verbena hastata	Craine et al. 2001			Stevens 1932	

APPENDIX A.2

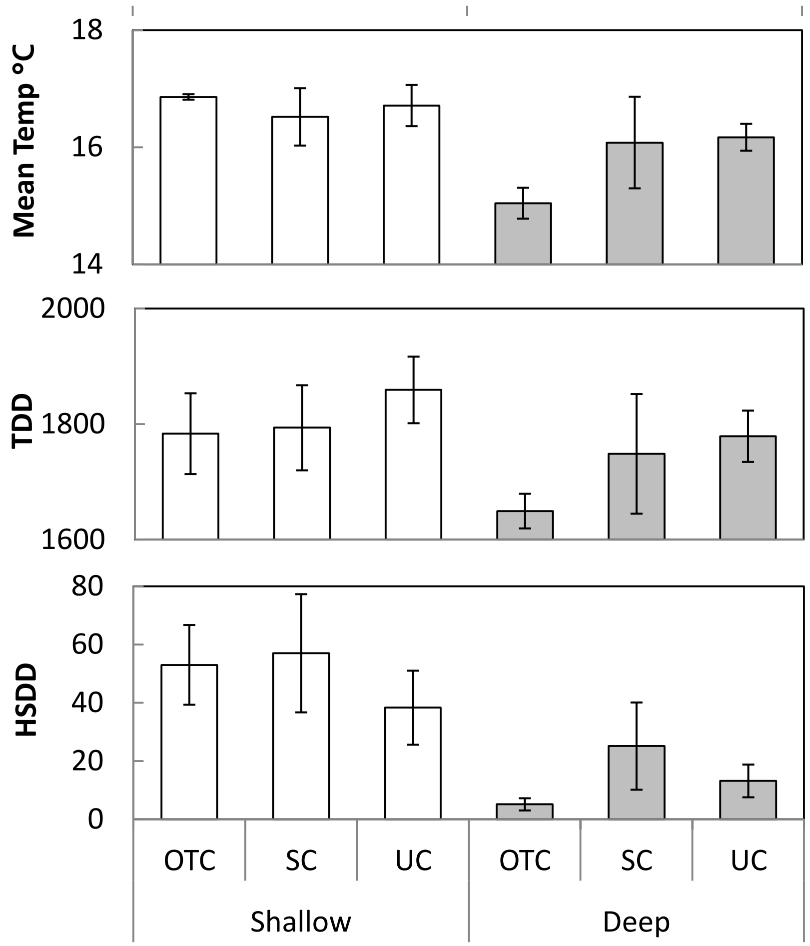
COMMUNITY-AGGREGATED FUNCTIONAL TRAIT DATABASE PRECISION ESTIMATES

Values reported in the table below are percent of total plant cover for all plot-level observations with literature reported values for species, for congeners, and missing data (from Appendix A.1).

	SLA	Height	Seed Mass
Species	60%	78%	97%
Congener	30%	0%	1%
Missing	10%	22%	2%

APPENDIX B.1

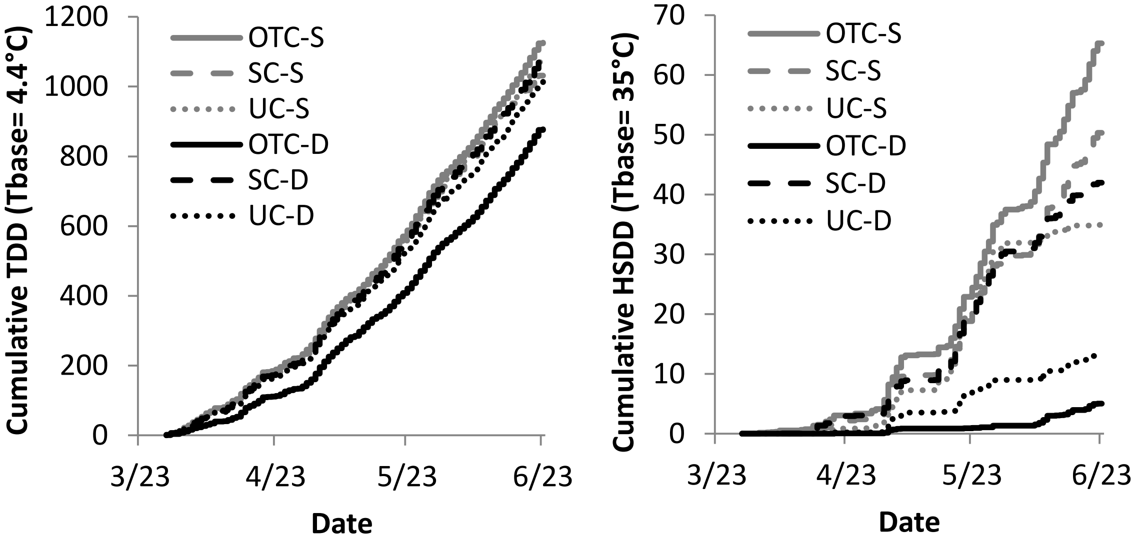
TEMPERATURE RESPONSES TO TREATMENT AND DEPTH



Bars represents means for a subset of plots that were instrumented with thermal dataloggers (n=3 per bar). Mean temperature (°C), Total Degree Days (TDD) = $\sum_{4.4°\mathrm{C}}(Tobs - 4.4°\mathrm{C}) * Time$ and accumulated heat stress degree days (HSDD) = $\sum_{35°\mathrm{C}}(Tobs - 35°\mathrm{C}) * Time$ were calculated for plots containing consistent records during the observation period (March-September)(see (Morrison & Stewart 2002) for a similar heat accumulation index).

APPENDIX B.2

TRADITIONAL DEGREE DAY ACCUMULATION CURVES



Total degree day (TDD) and heat stress degree day (HSDD) accumulation curves are represented for the 2012 growing season. Total Degree Days (TDD) = $\sum_{4.4°\mathrm{C}}(Tobs - 4.4°\mathrm{C}) * Time$ and accumulated heat stress degree days (HSDD) = $\sum_{35°\mathrm{C}}(Tobs - 35°\mathrm{C}) * Time$ were calculated for plots containing continuous records during the observation period (March-June) before the first major data gap resulting from instrument failure. Lines represent values reported at 30 minute intervals for the period March-June and 1 hour intervals for the period July-September.

APPENDIX B.3.

TWO-WAY ANOVA RESULTS FOR SEED METRICS

Metrics with a (*) indicate a Welch's test was used to determine significance as model residuals indicated significant heteroscedasticity (Bartlet's test p<0.05).

Metric	Comparison	DF	F	P-value
SLA (cm2/g)	***MEAN***	*3,27*	*0.4908*	*0.6916*
	Depth	1	0.0034	0.9543
	Plot Type	2	0.7345	0.4891
Height (cm)	***MEAN***	*3,27*	*3.596*	*0.0263†*
	Depth	1	9.9246	0.004‡
	Plot Type	2	0.4112	0.667
****CH/CL Ratio***	***MEAN***	*3,27*	*5.9568*	*0.0031†*
	*Depth	1	37.366	<0.0001‡
	Plot Type	2	0.4449	0.6457
Seed Mass (mg)	***MEAN***	*3,27*	*0.22*	*0.8816*
	Depth	1	0.0386	0.8456
	Plot Type	2	0.3094	0.7365
	****CH***	*3,27*	*0.4395*	*0.7267*
	Depth	1	0.0042	0.9487
	Plot Type	2	0.6541	0.5282
	****CL***	*3,27*	*1.7455*	*0.1814*
	Depth	1	4.7488	0.0382
	Plot Type	2	0.2432	0.7858

(cont.) Metrics with a (*) indicate a Welch's test was used to determine significance as model residuals indicated significant heteroscedasticity (Bartlet's test p<0.05).

Metric	Comparison	DF	F	P-value
Seed Mass per Ramet (mg)	***TOTAL***	*3,27*	*3.3901*	*0.0323*
	Depth	1	8.6548	0.0066
	Plot Type	2	0.7345	0.4891
	CH	*3,27*	*3.7983*	*0.0215*
	Depth	1	11.3854	0.0023
	Plot Type	2	0.0037	0.9963
	CL	*3,27*	*2.014*	*0.1357*
	Depth	1	0.2065	0.6532
	Plot Type	2	2.9103	0.0717
Seed Count per Ramet (#)	***TOTAL***	*3,27*	*7.3124*	*0.001†*
	Depth	1	20.3662	0.0001‡
	Plot Type	2	0.7595	0.4777
	CH	*3,27*	*11.7075*	*<.0001†*
	Depth	1	33.8201	<.0001‡
	Plot Type	2	0.6385	0.5359
	****CL***	*3,27*	*0.87*	*0.4687*
	Depth	1	2.0364	0.165
	Plot Type	2	0.2967	0.7457

APPENDIX B.4.
MEAN VALUES FOR SEED CHARACTERISTICS

Mass/seed reflects resource investment per propagule, seed/ramet (mg) reflects the amount of resources allocated by each ramet for reproduction via seed, and seed/ramet (count) reflects the number of potential offspring produced per ramet.

	Seed	Shallow			Deep		
	Type	**OTC**	**SC**	**UC**	**OTC**	**SC**	**UC**
Mass/Seed (mg)	**Mean**	0.06	0.05	0.05	0.04	0.06	0.06
	Chas	0.04	0.05	0.04	0.02	0.05	0.06
	Clei	0.12	0.09	0.1	0.06	0.05	0.05
Seed/Ramet (mg)	**Total**	22.98	20.53	19.85	14.3	12.12	9.91
	Chas	12.2	13.77	13.73	5.39	5.79	4.93
	Clei	10.78	6.75	6.12	8.91	6.33	4.98
Seed/Ramet (Count)	**Total**	368	379	392	397	255	191
	Chas	280	302	328	236	119	89
	Clei	89	77	64	161	136	102

APPENDIX B.5.

PERCENT RELATIVE ABUNDANCE ESTIMATES GENERATED USING THE POINT-INTERCEPT METHOD (2012)

Subscripts indicate sample size. Plots are ordered by overall mean abundance.

	Shallow$_{n=18}$			**Deep$_{n=16}$**			
Species	**UC$_6$**	**SC$_6$**	**OTC$_6$**	**UC$_5$**	**SC$_5$**	**OTC$_6$**	**Grand Mean**
Leersia oryzoides (L.) Sw.	69	62	85	24	64	64	61
Polygonum pennsylvanicum L.	15	36	14	14	12	10	17
Bidens aristosa (Michx.) Britton	11	<0.5	0	43	8	0	10
Sparganium eurycarpum Engelm.	0	0	0	16	17	24	10
Juncus effusus L.	2	0	0	2	0	0	1
Polygonum sagittatum L.	1	1	<0.5	0	0	0	<0.5
Phalaris arundinacea L.	2	0	0	0	0	0	<0.5
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	0	0	0	0	0	1	<0.5
Sagittaria latifolia Willd.	0	0	0	1	0	0	<0.5
Polygonum hydropiperoides Michx.	0	0	<0.5	0	0	0	<0.5
Carex hystericina Muhl. ex Willd.	0	0	0	0	0	0	0
Carex scoparia Schkuhr ex Willd.	0	0	0	0	0	0	0

APPENDIX B.6.

RESULTS OF SIMPER ANALYSES BASED ON BRAY-CURTIS COEFFICIENTS

Contrib. % represents the % of variation in each species responsible for differences between structure types (i) or depths (ii). Cum. % is a running total of Contrib. %, indicating the total percentage of variation among plots explained by a species combined with the species listed above it.

i. SIMPER : Structure Type (Cum. Diss. = 43)	**Contrib. %**	**Cum. %**	**Relative Cover %**		
Species			**UC**	**SC**	**OTC**
Leersia oryzoides (L.) Sw.	36	36	48	63	75
Polygonum pennsylvanicum L.	23	59	15	25	12
Bidens aristosa (Michx.) Britton	21	81	26	4	0
Sparganium eurycarpum Engelm.	15	96	7	8	12
Juncus effusus L.	1	98	2	0	0
Polygonum sagittatum L.	1	99	1	1	<0.5
Phalaris arundinacea L.	1	99	1	0	0
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	0	100	0	0	<0.5
Sagittaria latifolia Willd.	0	100	<0.5	0	0
Polygonum hydropiperoides Michx.	0	100	0	0	<0.5
Carex scoparia Schkuhr ex Willd.	0	100	0	0	0
Carex hystericina Muhl. ex Willd.	0	100	0	0	0

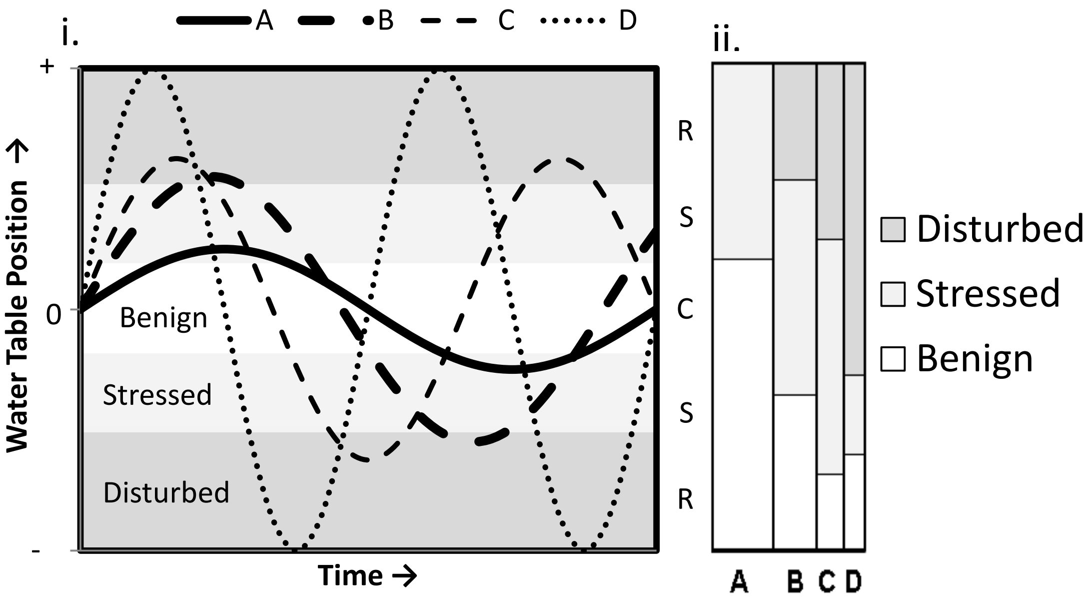
ii. SIMPER : Depth (Cum. Diss. = 46)	**Contrib. %**	**Cum. %**	**Relative Cover (%)**	
Species			**Shallow**	**Deep**
Leersia oryzoides (L.) Sw.	34	34	72	52
Polygonum pennsylvanicum L.	22	56	22	12
Sparganium eurycarpum Engelm.	21	77	0	20
Bidens aristosa (Michx.) Britton	19	96	4	16
Juncus effusus L.	1	98	1	1
Polygonum Sagittatum L.	1	99	1	0
Phalaris arundinacea L.	1	99	1	0

(cont.) Contrib. % represents the % of variation in each species responsible for differences between structure types (i) or depths (ii). Cum. % is a running total of Contrib. %, indicating the total percentage of variation among plots explained by a species combined with the species listed above it.

ii. SIMPER : Depth (*continued*) (Cum. Diss. = 46)	**Contrib. %**	**Cum. %**	**Relative Cover (%)**	
Species			**Shallow**	**Deep**
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	<0.5	100	0	<0.5
Sagittaria latifolia Willd.	<0.5	100	0	<0.5
Polygonum hydropiperoides Michx.	<0.5	100	<0.5	0
Carex scoparia Schkuhr ex Willd.	0	100	0	0
Carex hystericina Muhl. ex Willd.	0	100	0	0

APPENDIX C.1

A CONCEPTUAL MODEL



(i.) describes the affects of simultaneously increasing water table amplitude and frequency (A-D) on the stress-disturbance regime. Rising amplitude and frequency bring vegetation in contact with three classes of environmental adversity consisting of conditions that are benign—productivity would be maximized in monoculture, stressed—growth is suboptimal, or disturbed—plant tissues are removed or irreversibly damaged. Grime's CSR strategies favored by each adversity class are indicated on the right edge of i. (ii.) presents the integrated proportion of time each hydrologic regime experiences the three classes of environmental adversity (vertical) which is in principle proportional to the selection intensity for each of the three strategies outlined in CSR theory, and the mean duration spent in any given adversity class (column width).

APPENDIX D.1

MODEL VARIABLE DESCRIPTIONS AND MEANS (N=3686).

	Variable	Description	Mean
Geog.	ELEVMN	Mean Elevation (m)	288.6
	ELEVMIN	Minimum Elevation (m)	249.13
	ELEVMAX	Maximum Elevation (m)	332.37
	ELEVSTD	Std Dev. Elevation (m)	15.57
	NEAR_DIST	Distance to nearest major river (km)	8.72
Land Cover	LCVR1	Urban and Built-Up Land (% Area)	1.45
	LCVR2	Dryland Cropland and Pasture (% Area)	38.43
	LCVR5	Cropland/Grassland Mosaic (% Area)	15.45
	LCVR6	Cropland/Woodland Mosaic (% Area)	17.98
	LCVR7	Grassland (% Area)	0.3
	LCVR10	Savanna (% Area)	0.54
	LCVR11	Deciduous Broadleaf Forest (% Area)	13.57
	LCVR14	Evergreen Needleleaf Forest (% Area)	0.76
	LCVR15	Mixed Forest (% Area)	10.09
	LCVR16	Water Bodies (% Area)	1.39
Human Impact	MEANhuman	Mean Human Footprint Index (Range 0-100)	39.55
	MINhuman	Minimum Human Footprint Index (Range 0-100)	17.04
	MAXhuman	Maximum Human Footprint Index (Range 0-100)	88.19
	STDhuman	Std. Dev. Human Footprint Index (Range 0-100)	14.56

		Variable	Description	Mean	A1B 2100	A2 2100
Climate	Temp	bio1	Annual mean temperature (°C)	12.02	13	14.16
		bio2	Mean diurnal temperature range (°C)	12.02	11.06	10.81
		bio3	Isothermality (Bio02 ÷ Bio07)	0.29	0.3	0.29
		bio4	Temperature seasonality (C of V)	0.04	0.03	0.03
		bio5	Max temperature of warmest week (°C)	28.74	33.14	34.3
		bio6	Min temperature of coldest week (°C)	-12.54	-3.92	-2.71
		bio7	Temperature annual range (Bio05-Bio06) (°C)	41.29	37.05	37.01
		bio8	Mean temperature of wettest quarter (°C)	18.93	19.46	19.89
		bio9	Mean temperature of driest quarter (°C)	-4.46	5.2	8.3
		bio10	Mean temperature of warmest quarter (°C)	20.86	25.09	26.22
		bio11	Mean temperature of coldest quarter (°C)	-5.03	1.42	3.09
	Precip	bio12	Annual precipitation (mm)	872.19	893.32	898.9
		bio13	Precipitation of wettest week (mm)	24.69	27.47	28.62
		bio14	Precipitation of driest week (mm)	7.88	8.48	8.1
		bio15	Precipitation seasonality (C of V)	0.34	0.33	0.35
		bio16	Precipitation of wettest quarter (mm)	301.4	312.36	318.4
		bio17	Precipitation of driest quarter (mm)	126.07	140.09	140.8
		bio18	Precipitation of warmest quarter (mm)	289.82	274	268.4
		bio19	Precipitation of coldest quarter (mm)	127.2	146.82	151.8

		Variable	Description	Mean	A1B 2100	A2 2100
Climate	Radiation	bio20	Annual mean radiation (W m-2)	133.6	133.03	132.9
		bio21	Highest weekly radiation (W m-2)	217.02	232.6	237.6
		bio22	Lowest weekly radiation (W m-2	51.58	44.65	42.76
		bio23	Radiation seasonality (C of V)	0.43	0.49	0.51
		bio24	Radiation of wettest quarter (W m-2)	196.58	194.3	193.2
		bio25	Radiation of driest quarter (W m-2)	72.05	78.8	85.79
		bio26	Radiation of warmest quarter (W m-2)	202.82	210.37	212.2
		bio27	Radiation of coldest quarter (W m-2)	68.52	57.4	55.04
	Soil Moisture	bio28	Annual mean moisture index	0.84	0.76	0.75
		bio29	Highest weekly moisture index	0.99	1.02	1.03
		bio30	Lowest weekly moisture index	0.62	0.47	0.43
		bio31	Moisture index seasonality (C of V)	0.14	0.24	0.27
		bio32	Mean moisture index of wettest quarter	0.96	0.96	0.96
		bio33	Mean moisture index of driest quarter	0.67	0.53	0.5
		bio34	Mean moisture index of warmest quarter	0.69	0.55	0.52
		bio35	Mean moisture index of coldest quarter	0.9	0.91	0.9
Resp	FWEPERCENT		Freshwater Emergent Wetland (% Area)	1.89		
	FSSPERCENT		Forested/Scrub-shrub Wetland (% Area)	6.39		

APPENDIX D.2

LINEAR MODEL SUMMARIES (AIC REDUCTION APPLIED) FOR EMERGENT WETLANDS

Variable	Estimate	Standard Error	t-value	VIF	Significance
(Intercept)	34.34	3.35	10.26	NA	***
XCoord	-0.14	0.02	-9.02	66.1	***
YCoord	-0.15	0.05	-3.11	341.9	**
ELEVMN	0	0	-8.1	39	***
ELEVMIN	0	0	8.8	37.6	***
ELEVMAX					
ELEVSTD	0	0	1.64	3.3	
LCVR1	-0.34	0.18	-1.89	2.4	.
LCVR2	-0.63	0.12	-5.08	44	***
LCVR5	-0.3	0.13	-2.26	10.5	*
LCVR6	-0.26	0.12	-2.11	19.3	*
LCVR10	-0.85	0.36	-2.33	1.5	*
LCVR11	-0.36	0.13	-2.71	24.7	**
LCVR15	-0.67	0.13	-5.06	13.3	***
MAXhuman	-0.01	0	-5.26	2.5	***
STDhuman	0.02	0	4.62	2.3	***

Variable	Estimate	Standard Error	t-value	VIF	Significance
bio3	-38.97	2.87	-13.56	86.3	***
bio4	-722.4	49.79	-14.51	692.8	***
bio5	-0.46	0.08	-5.73	398.6	***
bio6	-0.66	0.04	-14.85	766.3	***
bio8	-0.07	0.01	-5.26	13.8	***
bio9	0.04	0.02	2.31	138.9	*
bio10	0.63	0.09	6.79	638.9	***
bio12	0	0	2.4	372.9	*
bio13	0.03	0.02	2.31	21.2	*
bio14	0.07	0.03	2.42	192.7	*
bio16	-0.01	0	-4.52	84.4	***
bio17	-0.02	0	-4.27	950.6	***
bio18	0.04	0	14.2	96	***
bio19	0.02	0	4.48	900.1	***
bio20					
bio21	-0.05	0.01	-5.29	54.5	***
bio22	-0.1	0.01	-10.29	140.9	***
bio23					
bio24	0.01	0	7.17	14.8	***
bio25	-0.01	0	-2.13	67.5	*
bio26	0.03	0.01	2.65	56.2	**
bio30	-9.21	0.81	-11.4	55.5	***
bio31	11.6	2.01	5.76	165.4	***
bio32	-9.27	1.21	-7.66	364.1	***
bio33	14.98	1.23	12.18	117.4	***
bio34	-16.48	1.29	-12.8	113.5	***
bio35	3.31	0.56	5.88	143.8	***

APPENDIX D.3

LINEAR MODEL SUMMARIES (AIC REDUCTION APPLIED) FOR FORESTED WETLANDS

Variable	Estimate	Standard Error	t-value	VIF	Significance
(Intercept)	-38.55	5.55	-6.95	NA	***
XCoord	-0.34	0.03	-13.1	65.2	***
YCoord	-0.22	0.09	-2.44	443.3	*
ELEVMN	-0.01	0	-8.23	61.1	***
ELEVMIN	0.01	0	12.46	41	***
ELEVMAX	-0.01	0	-6.74	48.3	***
ELEVSTD	0.01	0	3.74	7.1	***
LCVR1	-0.79	0.22	-3.54	1.3	***
LCVR2	-0.91	0.09	-9.68	9	***
LCVR5	-0.65	0.11	-5.9	2.6	***
LCVR6	-0.63	0.09	-6.74	4	***
LCVR10					
LCVR11	-0.62	0.11	-5.49	6.6	***
LCVR15					
MAXhuman	0.01	0	2.57	2.5	*
STDhuman	-0.03	0.01	-4.42	2.3	***

Variable	Estimate	Standard Error	t-value	VIF	Significance
bio3	-22.52	4.33	-5.2	69.8	***
bio4	-1167	82.31	-14.17	674.3	***
bio5					
bio6	-1.05	0.07	-14.7	697	***
bio8	-0.02	0.01	-1.72	5.6	.
bio9	0.1	0.03	3.91	132.1	***
bio10	0.68	0.11	6.08	332.2	***
bio12					
bio13					
bio14	0.37	0.05	8.14	182	***
bio16	-0.03	0	-11.55	38	***
bio17	-0.03	0	-6.49	281.3	***
bio18	0.03	0	7.94	65.3	***
bio19					
bio20	0.26	0.04	7.23	426.6	***
bio21	-0.1	0.02	-4.34	110.7	***
bio22					
bio23	78.72	6.48	12.14	492.5	***
bio24					
bio25	-0.02	0.01	-3.22	57.8	**
bio26	-0.05	0.02	-2.65	63.4	**
bio30					
bio31	17.72	1.69	10.47	41.6	***
bio32	6.23	1.41	4.42	176.4	***
bio33					
bio34	5.16	1.43	3.6	50.1	***
bio35	-3.8	0.88	-4.34	124	***