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ORIGINAL RESEARCH

Shrub Encroachment Increases Transpiration Water Loss from a Subtropical Wetland

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Abstract Encroachment of woody shrubs into graminoid-dominated wetlands can impact ecosystem carbon and water cycling due to differences in species physiology. In subtropical Florida, shortened hydroperiods have led to the expansion of Carolina willow (*Salix caroliniana*) in sawgrass (*Cladium jamaicense*) marsh communities, potentially compromising ecosystem health. In this study, we assessed differences in leaf gas exchange between willow and sawgrass in Blue Cypress Marsh Conservation Area (BCMCA). Stomatal conductance (g_s) and photosynthetic CO_2 exchange (A_{net}) were measured across a range of photosynthetically active radiation (PAR; 0–2000 μmol m^{-2} s^{-1}). Leaf area index (LAI; m^2 leaf m^{-2} ground) was determined for each species and used in conjunction with land cover estimates to extrapolate leaf measurements to the plant canopy and assess the consequences of shrub encroachment on landscape atmospheric carbon and water exchange. Willow had higher average rates of leaf g_s and A_{net} than sawgrass. However, willow had lower water use efficiency (WUE) and greater LAI, resulting in greater loss of water through transpiration by willow populations and diminishing projected landscape water availability despite marginally increased C assimilation. Climate drying or potential positive feedbacks of shrubs to autogenic drying may accelerate shrub encroachment and increase risk of wetland loss.

Keywords Carbon cycling · Everglades · Invasion ecology · Land cover change · Photosynthesis · Peatland · Shrub encroachment · Water use efficiency

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Introduction

Wetlands are critical ecosystems with many important ecosystem services including floral and faunal biodiversity, surface water storage and groundwater recharge, flood mitigation, and carbon storage (Finlayson et al. 1999; Mitsch and Gosselink 2007; Zedler and Kercher 2005). Wetlands are characterized by a tight linkage between hydrology, soils, and vegetation; as such, disruption to one of these links can compromise the entire ecosystem. Perturbations of wetlands have resulted in loss of nearly half of wetland land cover globally, largely as a result of human activity (MEA 2005; Zedler and Kercher 2005). It is therefore crucial we understand the direct and indirect implications of alterations to wetlands in order to assess their vulnerability and resilience to natural or anthropogenic disturbances.

Herbaceous graminoid-dominated marshes are common wetland types globally, and the subtropical marshes of south Florida (e.g.: Florida Everglades, Upper St. Johns River Basin) typify the stresses imposed on wetlands by hydrologic alterations and anthropogenic pressures. Decades of water management and development have degraded much of Florida's natural wetland ecosystems (Ogden 2005; Givnish et al. 2008), causing concern for the quality and quantity of water within Florida watersheds (Mitsch and Gosselink 2007; Dahl 2005) and facilitating exotic and native species invasions (Light and Dineen 1994). The resulting changes in land cover affect foraging and nesting habitat for wading and migratory game birds (Ma et al. 2010; Pierce and Gawlik 2010), soil and water nutrient loading (Waters et al. 2012), and above and below ground carbon storage (Bodel et al. 1994; Martin et al. 2009).

Sawgrass (*Cladium jamaicense*) is a characteristic sedge of subtropical freshwater wetlands of Florida (Loveless 1959; Craighead 1971), although its distribution spans from more

northern temperate wetlands to equatorial tropical biomes. In the Everglades, sawgrass forms nearly monotypic plains or emergent raised ridges characteristic of the patterned ridge-slough landscape (Craighead 1971; Wade et al. 1980). It is best adapted to grow in deep organic peat soils with low nutrient and soil oxygen availability and long hydroperiods (Steward and Ornes 1975; Wade et al. 1980; Schedlbauer et al. 2012) although sawgrass can withstand seasonal water level fluctuations (Wade et al. 1980; Schedlbauer et al. 2012). However, anthropogenic manipulation of Florida wetlands has altered natural hydrologic regimes, compromising the internal drivers of sawgrass community maintenance and providing opportunities for other native plant species to increase in abundance or for exotic invasive plants to become established (Kinser et al. 1997; Watts et al. 2010).

While woody shrubs are common in many herbaceous wetlands, they are typically low in abundance and often limited to drier margins or raised features. Carolina willow (*Salix caroliniana*) is a shrub native to Florida's wetlands, typically restricted to small, sporadic patches or elevated areas like tree islands where they take advantage of wetland soils that become exposed either seasonally or following drought or disturbance events. They are shade intolerant and grow rapidly, forming dense stands that often exclude herbaceous wetland vegetation by shading the understory while promoting other woody plants (NPS 2006; Ponzio et al. 2006).

Willow and other woody shrubs (both native and exotic) have been invading herbaceous wetlands throughout Florida (Bodel et al. 1994; Martin et al. 2009; Quintana-Ascencio et al. 2013) as well as other low-latitude wetlands globally (Cook et al. 1996; Rundel et al. 2014). While the extent of most types of wetlands has been declining in the United States, shrub wetland cover has been increasing (Dahl 2011). In Florida alone 116,150 ha of herbaceous wetlands were replaced by shrub wetlands in the 1990s (Dahl 2005). The expansion of willow in many subtropical wetlands has been attributed to fire suppression (Lee et al. 2005a, b) and shortened hydroperiods in a landscape fragmented by the construction of levees and canals (Quintana-Ascencio et al. 2013). Wetland shrub encroachment is undesirable as it can reduce landscape heterogeneity, biodiversity, and ecological and economic services (Kinser et al. 1997; Ponzio et al. 2006; Quintana-Ascencio et al. 2013). Once established, the altered habitat conditions created have a positive feedback to the spread and persistence of willow, particularly though diminished fine fuel loading necessary to support the fires (natural and prescribed) that maintain herbaceous sawgrass-dominated communities (Kinser et al. 1997) and through autogenic drying of surface soils (Doody et al. 2011) making unsuitable habitat conditions for most wetland plants.

Land cover change can affect wetland ecosystem dynamics due to ecophysiological differences between shrubs and graminoids. Compared to thin erect leaves of sawgrass and other graminoids, broadleaf plants such as willow have greater leaf surface area with more potential for photosynthetic carbon assimilation and transpiration water loss (Table 1; Lambers et al. 2006; Barger et al. 2011; Boyce et al. 2012). Changes in local community composition and diversity can alter net primary productivity (NPP) and, subsequently, ecosystem carbon uptake (Barger et al. 2011). Additionally, the magnitude of the trade-off between photosynthetic gain (i.e., CO_2 fixation) and leaf water loss during CO_2 uptake (i.e., transpiration), expressed as leaf water use efficiency (WUE: Lambers et al. 2006), can vary greatly among plant species and have consequences for ecosystem coupled carbon and water cycling.

In this study we quantified leaf gas exchange (CO_2 and H_2O) of willow and sawgrass in a subtropical peatland to evaluate the impact of land cover change through shrub expansion on wetland ecosystem water and carbon cycles. We hypothesized that willow would have diminished WUE that, in conjunction with increased land cover, would significantly increase wetland water loss to the atmosphere.

Materials and Methods

Field Site Description

Research was conducted at Blue Cypress Marsh Conservation Area (BCMCA; 27° 39.75' N, −80° 38.53' W), a sawgrass peatland within the St. Johns River Water Management District (SJRWMD) located in Indian River County, FL. BCMCA is an 8,600 ha subtropical floodplain marsh with a long hydroperiod (9–12 months), holding water for all or most of the year (Hall 1987; Lee et al. 2005a). Soils are primarily histosols with peat depths of 1–4 m (Lee et al. 2005a). Vegetation is characterized by sawgrass, maidencane (*Panicum hemitomon*), and cattail (*Typha* spp.) marshes, cypress (*Taxodium distichum*) and red maple (*Acer rubrum*) tree islands, willow-dominated shrub swamps, and white water lily (*Nymphaea odorata*) and bladderworts (*Utricularia* spp.) in deep water areas (Kinser et al. 1997; Lee et al. 2005a). The hydrology, soil composition, and vegetation communities of BCMCA are similar to those that characterize the freshwater peatland of the Florida Everglades.

Leaf Gas Exchange Measurements

Photosynthetic capacity and stomatal conductance (g_s) were evaluated by measuring leaf gas exchange (CO_2 and H_2O) of willow and sawgrass plants in BCMCA. Using a portable photosynthesis system (LI-6400xt, LI-COR, Lincoln, NE, USA), photosynthetic light response data was collected by measuring net leaf carboxylation (A_{net}) and g_s across an irradiance gradient of photosynthetically active radiation (PAR;

Table 1 Comparison of physiological characteristics of sawgrass and willow

Species	Growth morphology	Stomatal conductance (mmol H_2O m^{-2} s^{-1})	Transpiration (mm day^{-1})
Sawgrass (*Cladium jamaicense*)	Perennial graminoid	152 ± 12[a]	3.16–5.93[b]
Willow (*Salix* spp.)	Deciduous woody broadleaf	~170[c]	1.54–16.34[d]

Willow data were compiled across multiple species

[a] Stomatal conductance of *C. jamaicense* from Koch and Rawlik (1993)

[b] Range of transpiration measured for *C. jamaicense* from studies by Mao et al. (2002) and Jiang et al. (2009)

[c] Stomatal conductance estimated from Fig. 1d in Aasamaa and Sõber (2012) for *Salix caprea*

[d] Range of transpiration measured for *Salix* sp. in studies by Cermak et al. (1984); Priban and Ondok (1986), Pauliukonis and Schnieder (2001); and Doody and Benyon (2011)

2000, 1600, 1200, 800, 600, 400, 200, 100, 50, and 0 μmol m^{-2} sec^{-1}). Each leaf was clamped inside the leaf chamber and allowed to acclimate at the highest level of PAR for 1–2 min before measurements began. Leaf temperature, CO_2 concentration, and H_2O mol fraction inside the leaf chamber were held constant based on ambient values within the chamber at the start of each leaf measurement. At each PAR level, measurements of net photosynthesis (A_{net}; the difference between total photosynthesis and the sum of photorespiration and dark respiration), and stomatal conductance (g_s; the rates of CO_2 entering and water exiting the leaf) were recorded after a minimum and maximum lag time of 120 and 200 s, respectively. Instantaneous leaf water flux measured as g_s was a proxy for transpiration because actual leaf water loss can not be measured using this method.

On each sampling day, light response data was collected from single leaves of different willow or sawgrass plants along a 30 m boardwalk within the marsh. Young, fully expanded leaves with no signs of wilting, folding, or other physical damage were selected to ensure results were from physiological processes and not an artifact of leaf condition. New leaves were selected on each sampling day, and collection of light response data was not repeated on previously measured leaves. In total 41 sawgrass and 46 willow leaves were sampled over 19 sampling days between June and November 2014, prior to willow seasonal leaf senescence, and we observed new leaves continually expanding until the end of November. Data were only collected on days with less than 50 % cloud cover between 9:00 and 14:00. Species were sampled on alternating days so the time of day of sampling was not systematically biased.

A modeled light response curve (LRC) was generated for willow and sawgrass by fitting the measured light response data from the 41 sawgrass and 46 willow leaves sampled to non-rectangular hyperbola, rectangular hyperbola, and exponential models using non-linear least squares regression (nlsLM; Elzhov et al. 2013). The model fit was compared using Akaike's information criterion (AIC; Mazerolle 2014) using R (R Core Team 2013); the lowest AIC values indicated the data best fit the rectangular hyperbola function:

$$A_{\mathrm{net}} = \left\{ \frac{A_{\max} \cdot \Phi \cdot \mathrm{PPFD}}{(\Phi \cdot \mathrm{PPFD}) + A_{\max}} \right\} + R_{\mathrm{d}} \quad (1)$$

representing net photosynthetic rate (A_{net}), irradiance-saturated photosynthetic rate ($A_{\max}$), photosynthetic quantum yield (Φ), photosynthetic photon flux density (PPFD), and the rate of dark respiration (R_{d}). The light compensation point (I_{c}; irradiance at $A_{\mathrm{net}} = 0$) and the light saturation point (I_{s}; irradiance at $A_{\max}$) were calculated based on the output of the fitted model.

Intrinsic water use efficiency (WUE) was calculated as the ratio of A_{net} (μmol CO_2 m^{-2} s^{-1}) to g_{s} (mol H_2O m^{-2} s^{-1}) collected at the highest PAR level (2000 μmol m^{-2} sec^{-1}). Statistical comparisons between willow and sawgrass for each of the measured (g_{s}, A_{net}, R_{d}), model fitted ($A_{\max}$, Φ), or calculated parameters (WUE, I_{c} and I_{s}) were made using t-tests in R.

To evaluate the representativeness of the plants selected for full light response curve data collection within the local populations at BCMCA, survey measurements of A_{net} and g_{s} were also measured from 30 willow and 29 sawgrass plants distributed throughout the marsh. Measurements were taken in October and November 2014 on young, undamaged leaves and the PAR level was set at 2000 μmol m^{-2} sec^{-1} to match the highest set point for comparison with the LRC data. Flow rate was kept constant at 500 μmol sec^{-1} and reference CO_2 was held at 400 μmol CO_2 mol^{-1}. Each leaf was clamped in the chamber for a minimum of 5 min and a maximum of 10 min and final values were logged when they were stable. Sample location coordinates were used to assess spatial autocorrelation (Moran's I statistic) to determine if physiological responses of each species differed based on marsh location. Values near −1 indicate regular patterning, values near 1 indicate clustering, and values near 0 indicate a random distribution. Additionally, t-tests were performed on A_{net} and g_{s} at maximum PPFD (2000 umol $m^{-2}sec^{-1}$) between the boardwalk and survey populations for each species to ensure the

plants sampled for light response curves were representative of the entire marsh.

Land Cover Change Projections

In 2001 and 2008, SJRWMD used aerial photographs and remote sensing techniques to measure the spatial extent of distinct plant communities at BCMCA (SJRWMD unpublished data). Land cover classes were defined by dominant plant species (Bryan and Miller 2004). The 'Sawgrass' and 'Willow Swamp' cover classes were defined as having at least 70 % dominance of sawgrass or willow, respectively, although dominant species cover was typically >70 % (K Ponzio, personal communication). To project landscape gas exchange in response to land cover change, we used the minimum dominant species coverage criteria (70 %) to conservatively estimate species-specific coverage of sawgrass and willow species within these cover classes.

To extrapolate leaf-level gas exchange to the landscape, leaf area indexes (LAI) were measured for sawgrass and willow at BCMCA. Aboveground biomass within 1 m^2 harvest plots was clipped at the soil surface for sawgrass (25 plots) and willow (6 plots). Total plot species leaf area was measured using an LI-3100C area meter (LI-COR, Lincoln, NE, USA) to quantify the total leaf area (m^2) per square meter of ground area. The average LAI of each species was multiplied by species land cover area for 2001 and 2008 to calculate total leaf area for each species. Total leaf area was multiplied by average net photosynthetic rate (A_{net}) and stomatal conductance (g_s) measured at PAR values of 2000 μmol m^{-2} sec^{-1} for willow and sawgrass to estimate the total gas flux for both populations (Table 2). Calculations were repeated for both survey years to evaluate the impact of willow encroachment (land cover change) on plant-mediated landscape water and carbon exchange.

Results

Leaf Gas Exchange

Photosynthetic light response curves (LRC, Fig. 1) and stomatal conductance differed between willow and sawgrass. Willow had higher average g_s ($T_{68}=-5.328$, $p<0.001$), A_{max} ($T_{82}=-3.081$, $p=0.003$), and Φ ($T_{76}=-6.908$, $p<0.001$) than sawgrass (Table 3). Dark respiration (R_d, $T_{75}=1.394$, $p=0.168$), I_c ($T_{66}=-0.052$, $p=0.959$), and I_s ($T_{44}=0.944$, $p=0.350$) did not differ between the two species (Table 3). Willow had lower full light WUE (46.67 μmol CO_2 mol H_2O^{-1} ±2.450 at 2000 μmol m^{-2} sec^{-1} PAR) than sawgrass (55.94 μmol CO_2 mol H_2O^{-1} ±2.292; $T_{85}=2.764$, $p=0.007$).

No substantial differences were found between the intensively sampled plants along the boardwalk and the rest of the populations of each species at BCMCA. Full light A_{net} and g_s did not differ based on location within the marsh for either sawgrass (A_{net}: Moran's I=0.005, $p=0.806$; g_s: I=−0.211, $p=0.289$) or willow (A_{net}: I=−0.088, $p=0.651$; g_s: I=0.025 $p=0.726$). Similarly, the boardwalk and survey populations did not differ in A_{net} for either species (willow: $T_{69}=1.027$, $p=0.308$, sawgrass: $T_{67}=-0.139$, $p=0.890$) or in g_s for willow populations ($T_{82}=1.653$, $p=0.103$), although g_s was slightly higher for the boardwalk sawgrass population than the survey population ($T_{68}=2.012$, $p=0.048$).

Land Cover Change at BCMCA

From 2001 to 2008, the 'Willow Swamp' and 'Sawgrass' cover classes in BCMCA increased by 29 % and 8 %, respectively, primarily spreading into wetter cover class types such as 'mixed herbaceous marsh' (37 % decrease) and 'mixed shrub marsh' (8 % decrease), although there was no change in overall wetland area at BCMCA. Despite greater expansion of willow cover, sawgrass continued to have greater total land cover (Fig. 2a). Persistently drier conditions within BCMCA were likely responsible for increased shrub cover, as observations from land managers suggest that marsh exposure occurred more frequently during the period following water management changes in 1997 (Ponzio, personal communication).

The branched morphology of willow compared to erect sawgrass leaves produced a willow LAI that was more than double that of sawgrass (Table 2). When leaf gas exchange was extrapolated to the landscape using the species LAI and cover data, the rate of landscape net primary production increased by 72.65 mol CO_2 s^{-1} between 2001 and 2008, with

Table 2 Parameters used to estimate landscape-level gas flux of sawgrass and willow communities; net photosynthesis (A_{net}) and stomatal conductance (g_s) measured at PAR level 2000 μmol m^{-2} sec^{-1}, leaf area index (LAI), and the estimated spatial extent of sawgrass and willow species-specific coverage calculated from the 2001 and 2008 community surveys at BCMCA

Species	A_{net} (μmol CO_2 m^{-2} s^{-1})	g_s (mol H_2O m^{-2} s^{-1})	LAI (m^2 leaf m^{-2} ground)	Spatial extent (ha)	
				2001	2008
Sawgrass	12.52	0.240	0.792	1914.5	2061.7
Willow	14.81	0.359	1.773	890.62	1111.7

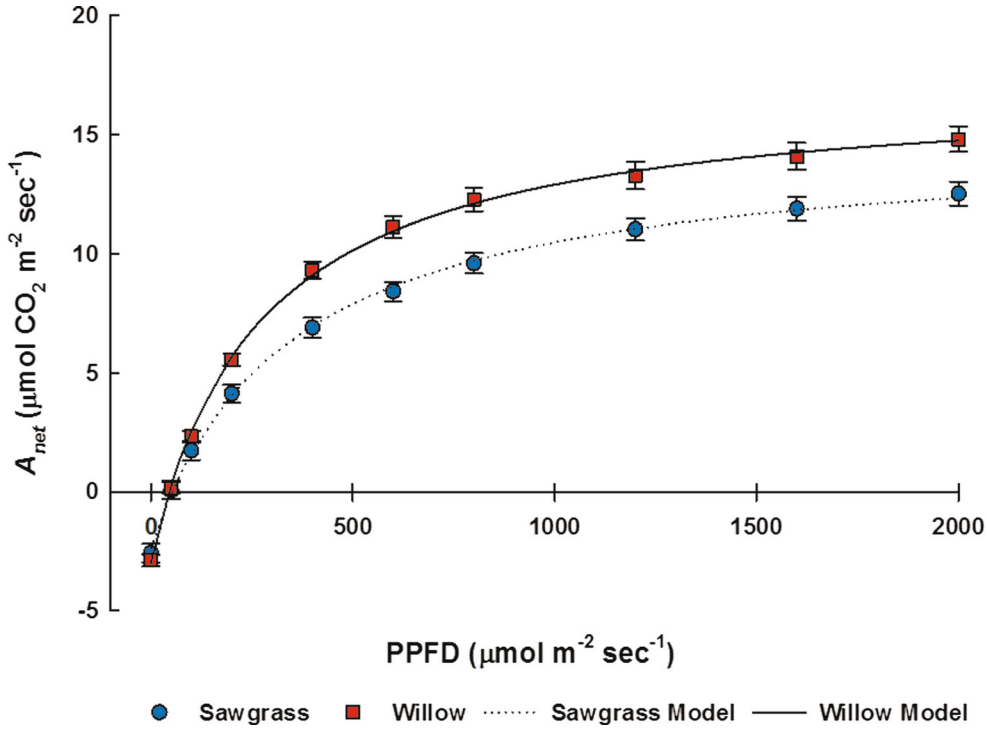

Fig. 1 Mean (±SE) leaf net photosynthetic assimilation (A_{net}) for sawgrass (*blue circles*) and willow (*red squares*) in response to photosynthetic photon flux density (PPFD). Lines represent fitted model curves based on Eq. 1 (parameter estimates provided in Table 3)

14.59 mol CO_2 s^{-1} increase from sawgrass and 58.06 mol CO_2 s^{-1} increase from willow (Fig. 2b). In the same period, the landscape rate of plant water loss increased by 1688.8 kmol H_2O s^{-1}, with a 280.26 kmol H_2O s^{-1} increase from sawgrass and 1408.5 kmol H_2O s^{-1} increase from willow (Fig. 2c). Willow had a disproportionate influence on landscape WUE despite half as much land cover as sawgrass (Table 2), with landscape WUE in 2001 (45.46 µmol CO_2 mol H_2O^{-1}) and in 2008 (45.09 µmol CO_2 mol H_2O^{-1}) more similar to the leaf WUE of willow (46.67 µmol CO_2 mol H_2O^{-1}) than that of sawgrass (55.94 µmol CO_2 mol H_2O^{-1}).

Discussion

Shrub encroachment can substantially impact wetland carbon and water cycling, which can compromise conservation and water management objectives. In this study, willow had more than double the leaf area of sawgrass and ~50 % greater transpiration per leaf, resulting in significant decline in landscape water use efficiency even with small increases in willow cover. While willow had greater carbon assimilation, indirect effects of water loss on wetland carbon cycling may counteract C assimilation gains. Aerobic soil conditions resulting from wetland drying accelerates soil decomposition (DeBusk and Reddy 2003; Qualls and Richardson 2008), potentially resulting in soil C losses exceeding the moderate gains in primary productivity.

While much of the expansion of shrubs in Florida's wetlands has been due to water management practices, climate change can induce similar changes in wetland hydrology and likely result in similar expansion of shrub land cover. Drier climate conditions from decreased precipitation or increased evapotranspiration due to increased temperatures can lead to a drier wetland landscape (Nungesser et al. 2015), which could further shrub encroachment. Additionally, autogenic soil drying resulting from increased transpiration water loss may be a positive feedback to willow spread, even in absence of

Table 3 Photosynthetic light response curve parameters for sawgrass and willow

Species	A_{net} (µmol CO_2 m^{-2} s^{-1})	g_s (mol H_2O m^{-2} s^{-1})	A_{max} (µmol CO_2 m^{-2} s^{-1})	Φ (mol CO_2 mol PAR^{-1})	R_d (µmol CO_2 m^{-2} s^{-1})	I_c (µmol m^{-2} s^{-1})	I_s (µmol m^{-2} s^{-1})
Sawgrass	6.461	0.152	17.47	0.052	−2.347	54.77	3008
Willow	8.032	0.230	20.57	0.078	−2.994	55.43	2562

Net photosynthesis (A_{net}) and stomatal conductance (g_s) were averaged across full range of PAR (0–2000 µmol m^{-2} sec^{-1}). Irradiance-saturated photosynthetic rate (A_{max}), photosynthetic quantum yield (Φ), and dark respiration (R_d) were estimated using Eq. 1. Light compensation point (I_c; irradiance at $A_{net}=0$) and light saturation point (I_s; irradiance at A_{max}) were calculated using the resulting model

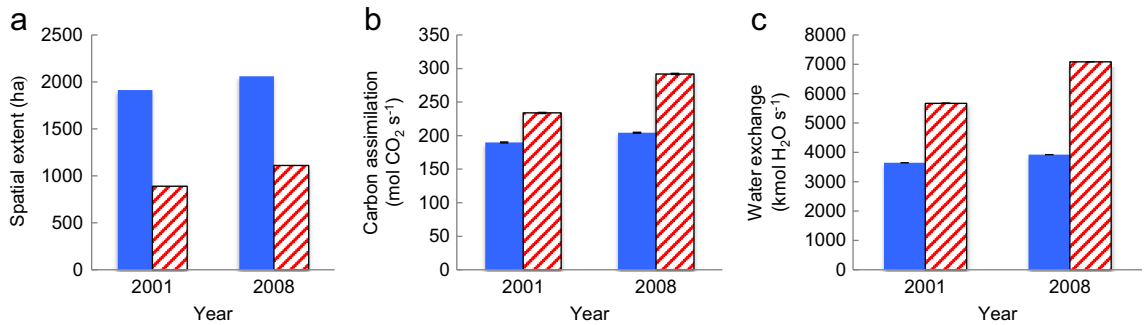

Fig. 2 Comparison of sawgrass (*solid blue*) and willow (*patterned red*) spatial extent (**a**) and extrapolated landscape A_{net} (± SE; **b**) and g_s (± SE; **c**). Carbon and water exchange were extrapolated using the estimated flux rates, land cover, and LAI from Table 2

anthropogenic or climate drying. Drier soil conditions promote willow seedling establishment and accelerate population spread (Kinser et al. 1997; Castro-Morales et al. 2014) and increase rates of willow photosynthesis and growth (Pezeshki et al. 1998), which contribute to even greater transpiration-driven soil drying.

Greater transpiration water loss will present challenges for maintaining standing-water conditions typical of these peatlands. These challenges may be magnified if the morphology (spreading, horizontal branches and leaves) and phenology (seasonally deciduous leaves) of willow alters evaporation in the canopy boundary layer. Willow rooting is also highly responsive and adaptive to changes in water table elevation and soil moisture. Riparian willows have been shown to produce adventitious roots in response to flooding (Pezeshki et al. 1998), while willow's phreatophytic roots are capable of accessing shallow water tables under drier wetland conditions (Busch et al. 1992; McLaughlin et al. 2012). This deep rooting would enable continued high transpiration and positive feedbacks to further soil drying, even under receding water tables.

Wetland drying coupled with shrub encroachment may catalyze successional shifts in plant community composition and ultimately wetland type. Willow and other shrubs are often found in early succession communities of forested swamps and peatlands (Craighead 1971; Van Breemen 1995; Mitsch and Gosselink 2007). Altered habitat conditions or disturbance regimes due to transition from an herbaceous to shrub dominated state may promote wetland afforestation or terrestrialization, potentially resulting in a persistently altered, and potentially unsustainable, ecosystem state (Zweig and Kitchens 2009; McLaughlin et al. 2012; Duever and Roberts 2013; Kettridge et al. 2015). Furthermore, drier soils and the erect woody stems of shrubs could facilitate the introduction of harmful exotic invasive plants like Brazilian pepper (*Schinus terebinthifolius*) or Old World climbing fern (*Lygodium microphyllum*), leading to further degradation of habitat quality, biodiversity, and ecosystem health within subtropical wetlands (LaRosa et al. 1992; Volin et al. 2004).

Shrub encroachment can have direct and indirect consequences for the health and resilience of freshwater wetlands under shifting climate conditions and changing land use. As much of mid- and low-latitude freshwater wetlands are subject to large anthropogenic pressures or active water management, conservation and land management activities should account for functional differences between shrubs and graminoids in wetlands when evaluating conservation priorities.

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