Scaling up experimental stress responses of grass invasion to predictions of continental-level range suitability

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Abstract. Understanding how the biological invasion is driven by environmental factors will improve model prediction and advance early detection, especially in the context of accelerating anthropogenic ecological changes. Although a large body of studies has examined how favorable environments promote biological invasions, a more comprehensive and mechanistic understanding of invasive species response to unfavorable/stressful conditions is still developing. Grass invasion has been problematic across the globe; in particular, C_4 grass invaders, with high drought tolerance, adaptations to high temperatures, and high water use efficiency, could become more severe. Here, we conducted a rigorous microcosm experiment, with one of the most damaging invasive C_4 grass, cogongrass (*Imperata cylindrica*), to explore how cogongrass responds to soil water and nutrient stress. We further integrated the results of the microcosm study with a species distribution model to (1) corroborate greenhouse results with field observations and (2) validate the robustness of our findings at subcontinental scales. Both the microcosm experiments and species distribution model agreed that soil water stress had a stronger impact on cogongrass than the nutrient one. New vegetative growth of cogongrass continued to be inhibited by the prior water stress. The significant water effect on cogongrass total biomass was supported by the finding that both allometric and biochemical traits of cogongrass did not show significant responses to the changes in water treatment. Different to the conventional wisdom that nutrient enrichment plays a bigger role in facilitating biological invasions, this study highlighted the possibility that water conditions may have a more substantial effect on some aggressive invaders. Therefore, an important implication of this study on biological conservation is that field managers might take advantage of the negative effect of global drought on some invasive species to increase the efficiency of their controlling efforts because invasive species may become more vulnerable under drought effect.

Key words: biological invasion; C_4 grass; cogongrass; microcosm experiment; nutrient stress; species distribution model; water stress.

Introduction

Biological invasions are becoming increasingly common with the accelerating impact of anthropogenic human activities and climate change (Simberloff et al. 2013, Wallingford et al. 2020). Invasive species affect

natural ecosystems via predation, competition, and habitat alteration and their management cost billions of dollars annually (Mack et al. 2000, Pimentel et al. 2000, 2005). A large body of research has emphasized the importance of predicting the conditions under which invasions are most likely to spread (Hulme 2017). Therefore, a fundamental understanding of how environmental factors drive invasion success can improve model prediction accuracy and advance early detection. Previous studies found that environments with greater nutrient availability often promote biological invasion because invasive plant species can rapidly assimilate available resources (Vitousek and Walker 1989, Huenneke et al. 1990, Dukes and Mooney 1999, Brooks 2003, Fenn et al. 2003, Eskelinen and Harrison 2014). Some invasive nitrogen-fixing plants can further accumulate soil nitrogen, thus leading to positive feedback that attracts more invasions (Ehrenfeld 2003, 2010). Despite the increasing environmental problems of global nitrogen deposition and drought (Bardgett and Wardle 2010, Bussotti et al. 2014), we know less about the interactive effects of water and nutrients on biological invasions (Burns 2004, Eskelinen and Harrison 2014, Schrama and Bardgett 2016). Investigations on invasive species' response to favorable and stressful conditions of soil nutrient and water availability will, therefore, provide a more holistic understanding of invasion success.

To improve survivorship under stressful environments, plants could make changes in their traits from the perspectives of allometry, biochemistry, and reproduction. Specifically, allometric changes focus on biomass allocation between above- and belowground organs of the plant. For example, with nutrient stress, more biomass is allocated to plant roots, leading to improved nutrient uptake (Hermans et al. 2006). Similarly, plants increase biomass allocation to roots in response to drought (Dong et al. 2014, Gargallo-Garriga et al. 2015, Valliere and Allen 2016b) because roots are metabolically activated to enhance the uptake of water and nutrients (Gargallo-Garriga et al. 2014). Another type of trait is biochemical traits related to ratios between plant chemicals (i.e., stoichiometry), e.g., foliar C:N would increase to reduce plant transpiration with water stress (Turner 1994, Urbina et al. 2015). Additionally, changes in reproduction traits represent another survival strategy across generations, i.e., to sustain the growth of future generations instead of the current one, stressed plants could allocate more biomass to reproduction and maintain its quality (e.g., maintain the number of resprouts in next growing season). The aforementioned changes in plant traits may make different contributions to plant survivorship. Therefore, identification of the trait changes that mostly contribute in stressful environments can improve mechanistic understanding of how invasive species persist under deficient nutrient and water environments.

Microcosms are ideal for conducting manipulative experiments to help deduce fundamental mechanisms of critical ecological processes and for testing hypotheses to gain a better understanding of landscape-level ecosystem function (Osmond et al. 2004, Spivak et al. 2011). However, results of microcosm studies have been questioned because the experimental conditions might not be robust enough to reflect a specific factor in a field (Kivlin et al. 2018), and they cannot be easily extrapolated across different types of ecosystems (Kerr and Ostrovsky 2003). Unlike microcosm studies, predictive species distribution models allow investigations of spatial correlations of invasive species and their current geographical distributions at larger spatial scales (He et al. 2011), and can predict species future distributions (Jennings 2000, Saveraid et al. 2001, He et al. 2015). Nonetheless, predictions solely based on species spatial distributions might be unreliable because of the limited extent, spatial resolution, and the low accuracy of collected data (Stohlgren et al. 1995). Consequently, integrating local experimental studies grounded on mechanisms with spatial distribution models focused on large-scale patterns can both corroborate greenhouse results with field observations and validate the robustness of results across multiple scales. To our knowledge, very few studies to date have attempted to compare the results of these two complementary methods to examine the consistency of invasive species' response to various environmental conditions across multiple spatial scales (Afkhami et al. 2014).

To investigate invasive species responses across a nutrient gradient paired with water availability gradient in both parent and offspring generations, we conducted a microcosm study with cogongrass (*Imperata cylindrica* (L.) P. Beauv.), which has been listed as one of the 100 worst invasive alien species in the world and listed as a Federal Noxious Weed in the United States (Lowe et al. 2000). Specifically, we used ^{15}N to track nutrient flow in both the above- and below-ground processes to examine whether environmental stress (nutrient and water) affects cogongrass through differential nutrient allocation. Furthermore, to assess if the mechanistic explanation from the microcosm experiment is consistent with cogongrass' geographical distribution with corresponding soil water and nutrient conditions, we compared the experimental results with patterns at the landscape scale via performing species distribution model analysis. Together, we address the following three questions: (1) What are the performance differences of cogongrass above- and belowground components, and vegetative reproduction under the interacting effects of water and nutrient stress? (2) Does cogongrass make changes in its allometric and biochemical traits to improve survivorship under stressing environment? (3) Are results from the microcosm experiments supported by the species distribution model analysis? If so, where will cogongrass likely invade in the future based on the results of our microcosm experiments and species distribution model analysis?

Methods and Materials

Cogongrass is native to tropical and subtropical areas of the Old World (Bryson and Carter 1993), and was introduced in 1912 from Japan (Bradley et al. 2010b, Burrell et al. 2015). Cogongrass is a warm-season, rhizomatous, perennial C_4 grass species that is found throughout the tropical and subtropical regions of the world (MacDonald 2004) and it is well adapted to full sunlight, frequent burning, and nutrient-poor soils (Holzmueller and Jose 2011). Cogongrass is an aggressive invasive grass, which spreads mainly via seeds and rhizomes (McConnaughay and Coleman 1999, MacDonald 2009). Due to its C_4 pathways, it can be drought tolerant, adapted to high temperatures, and also have greater water use efficiency, making it potentially more competitive in lower latitudes as compared to C_3 invaders. Since its initial introduction to the United States, cogongrass has expanded its range in the southeastern United States from Texas to Florida and as far north as Virginia (Jose et al. 2002) and it is considered a primary threat to biodiversity and ecosystem functions (Estrada and Flory 2015, Fahey et al. 2018, Alba et al. 2019).

Experimental design

Potted cogongrass were collected/obtained from the Entomology and Nematology Department greenhouse of at the University of Florida Gainesville, Florida, USA and relocated to a greenhouse at the Institute of Food and Agricultural Sciences (IFAS), University of Florida, Davie, Florida. All the cogongrass belonged to a same genotype that was originally collected in Florida and they grew in similar environments before (Enloe et al. 2018). Cogongrass rhizome samples were collected from the field then relocated to the greenhouse in IFAS. Additionally, based on a genotyping-by-sequencing approach to identify genetic diversity of cogongrass in the southeastern United States, Burrell et al. (2015) found each of the four clonal lineages of cogongrass was highly homogeneous and cogongrass has limited evolutionary potential. Therefore, the cogongrass lineage we used in this study could represent, at least, a main part of natural cogongrass populations. Cogongrass was propagated under ambient conditions for two months to adapt to the new environment before being used in our experiments.

All the experiments were performed in the same greenhouse in Davie, Florida. Greenhouse temperatures were maintained at 25°–30°C, corresponding roughly to ambient temperatures in the region. Single cogongrass rhizome fragments (≈15 cm in length with at least four nodes) were cut from the potted cogongrass plants. A single rhizome was transplanted horizontally into each pot and was placed in the center of the pot (25 cm upper diameter × 20 cm lower diameter × 23 cm height) filled with commercial potting mix (Fafard Professional Growing Mix, Sun Gro Horticulture Canada, Agawam, Massachusetts, USA). Note that the potting soil we used here contains Canadian sphagnum peat moss, bark, perlite, and vermiculite, while it does not contain any additional fertilizer. Pots were randomly assigned inside the greenhouse to account for microclimate conditions. All the pots received weekly watering until saturated for one month and only the pots with successful rhizome germination were used for later experiments.

Our experiment was a full factorial design consisting of two factors: water (low and high) and nutrient (low and high) frequencies. In the low-water treatment, water was applied to the soil surface until saturation every month (soil moisture ≈ 34% ± 7% [mean ± SD]) and, in the high-water treatment, water was provided every two weeks (soil moisture ≈ 90% ± 6%). The watering frequency was modified according to the watering frequency used in Webster and Grey (2008) to have a close representation of the weather in Florida, which also resulted in similar soil water contents to what Burns (2004) used in her study. Indeed, a further lower water level could be used to mimic a stronger drought (Burns 2004, Alba et al. 2019). Our watering frequency was designed based on a comprehensive consideration of watering period and soil water content to have a close representation of the weather in Florida, which also aimed to mimic meteorological drought to ultimately show vegetation physiological drought response. The low-nutrient treatment received no additional nutrient fertilizer across the entire experiment and the high-nutrient treatment received constant nutrient fertilizer every two weeks. Fertilizer was purchased from General Hydroponics (genhydro, Santa Rosa, California, USA). The fertilizer was dispensed into each pot according to the manufacturer's recommendations (total nitrogen 0.009%; P_2O_5 0.007%; K_2O 0.014%). Each treatment was replicated 11 times (total of 44 pots) (experimental setup is shown in Appendix S1: Fig. S1A and four randomly selected pots from each treatment are shown in Appendix S1: Fig. S1B). The total 44 pots were placed in a randomized complete block design in the greenhouse. The duration of the experiment was seven months from the beginning of September 2018 to the end of March 2019. We ran the experiment for seven months for two reasons. (1) Most similar experiments with cogongrass ran for 8–12 weeks to monitor the effects of environmental factors on cogongrass survival and growth (King and Grace 2000, Holly and Ervin 2007, Prince et al. 2018). Thus, we believe seven months would be long enough. (2) After six months, we observed a majority of cogongrass' aboveground biomass had dried out and we found almost no new germinations in the low-water treatments. Hence, we ran for another month to ensure there was no further change we would observe before we harvest the plants.

Sample collection and analysis

Carbon and nutrient (nitrogen) uptake was determined by the ^{15}N enrichment technique described by (Gessler et al. 1998). Only one of the N compounds present in the solution was ^{15}N labeled. The isotope tracer was added by putting 0.667 mg non-labeled K nitrogen and 0.333 mg labeled K nitrogen in each pot. A 5-cm piece of randomly selected foliage was cut with a sterilized scissor from each pot five times. The sampled foliage from each pot was stored in separate brown envelopes and transported to a laboratory at the University of Miami for analyses. To quantify total carbon (C), nitrogen (N), and δ^{13}C and δ^{15}N enrichment, we first oven-dried samples at 60°C for 48 h to constant mass and ground samples to a fine homogenous powder using a ball mill (TissueLyser, Retsch, Haan, Germany). We then loaded 5 mg of foliage into tin cups (5 × 8 mm; Elementar Americas, Mt. Laurel, New Jersey, USA) for measurements of isotopic compositions of C and N. The samples were then analyzed by an automated elemental analyzer (Pyro Cube; Elementar, Hanau, Germany) connected to a continuous flow isotope ratio mass spectrometer (Isoprime, Stockport, UK) at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems at the University of Miami following the methods of Wang et al. (2011). Foliar C (C%) and N (N%) content were measured as a mass percentage of total foliar C and N relative to total leaf dry mass. Isotopic compositions, as δ^{13}C and δ^{15}N values, were expressed as

$$\delta^{13}C(‰) \text{ or } \delta^{15}N(‰) = \left[\left(R_{sample}/R_{standard} \right) - 1 \right] \times 1000 \tag{1}$$

where R_{sample} is the C or N stable isotope ratio (i.e., $^{13}C/^{12}C$, $^{15}N/^{14}N$) of the sample of interest, and $R_{standard}$ is the value of the corresponding international reference standard (Vienna Pee Dee Belemnite formation of South Carolina for carbon and atmospheric N_2 for nitrogen). The precision of the %N analysis was ±1 ppm (±SD) and the precision of the C and N isotopic analysis was ±0.1‰ (±SD).

We harvested all the plants in the beginning of April 2019 and separated the above- and belowground biomass. Before drying the root biomass, we cut three randomly selected rhizome tips (≈1 cm in length) with a sterilized scissor in each pot at harvest time for examining root total carbon (C), nitrogen (N), and δ^{13}C and δ^{15}N enrichment. We used the same protocol as we performed with the foliage. To determine if the vegetative reproduction of the same generation was affected by prior water and nutrient treatments, three randomly selected rhizome fragments (≈15 cm in length with at least four nodes) of the harvested plants in each pot were cut and replanted horizontally into a new pot (25 cm upper diameter × 20 cm lower diameter × 23 cm height) filled with the same commercial potting mix

(Fafard Professional Growing Mix, Sun Gro Horticulture Canada, Agawam, Massachusetts, USA). All the pots were watered similarly to saturation from the top for five weeks until the number of new sprout stopped changing. Total number of new sprouts was counted in each pot.

Belowground biomass was carefully cleaned with tap water to ensure that hardly any soil particles remained attached to the rhizomes. Above- and belowground parts were stored in different brown envelopes and oven-dried at 60°C for 72 h until constant mass was reached and then were weighed with and electronic balance to obtain dry biomass (g).

Data analysis

Total biomass and number of sprout as a function of water and nutrient treatments.—Linear mixed-effected model (LMEM) was used to analyze the effects of water and nutrient on total biomass (Eq. 2). Generalized linear model (GLM) based on Poisson distribution was used to analyze the effects of water and nutrient on number of sprouts, and there is a logarithmic link in the Eq. 3 between the mean of $G_{i,j}$ and the predictor function.

$$TB_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_{3,i,j} \times W_i \times N_j + \beta_0 + \alpha_k + \varepsilon_i, \ \varepsilon_i \sim N\left(0, \sigma_i^2\right) \tag{2}$$

$$\log(G_{i,j}) = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon, \ \varepsilon \sim N\left(0, \sigma^2\right) \tag{3}$$

where $TB_{i,j}$ and $G_{i,j}$ were the total biomass and number of sprouts at a given level of water (i) and nutrient (j), respectively. The parameter $\beta_{1,i}$ was the coefficient of W_i (the ith level of fixed water factor), $\beta_{2,j}$ was the coefficient of N_j (the jth level of fixed nutrient factor), $\beta_{3,i,j}$ was the coefficient of interaction of W_i and N_j, β_0 was the intercept, α_k was the random factor by kth table, ε_i and ε were the residual in the Eqs. 2 and 3, respectively, and ε_i assumed heterogeneity between the levels of water. The model selection and assumption examination followed the procedures in Zuur et al. (2009). The model selection was based on the Akaike information criterion (AIC) of models with different variance and covariance (or random) structures. The fixed-effect structure was determined by AIC calculated from maximum likelihood (ML), thus the interaction of water and nutrient on $G_{i,j}$ was removed, and then restricted maximum likelihood (REML) was used to estimate model parameters. The violation of normality in Eq. 2 was visually checked by a *Q-Q* plot. The dispersion parameter of Eq. 3 was 1.94, and a quasi-GLM was built to correct potential dispersion. But compared with the original model, the corrected one didn't change the significance level of predictors. The violation of homogeneity and independence

of both Eq. 2 and Eq. 3 were examined by checking residual plots along the fitted values and levels of water and nutrient. The above statistical analyses were made using the R program (Kuhn et al. 2020) and the nlme package (Pinheiro et al. 2012).

Allometric and biochemical traits as a function of water and nutrient treatments.—Multiple linear regression model (MLRM) or linear mixed-effected model (LMEM) was used to analyze the effects of water and nutrient on allometric and biochemical traits: aboveground : belowground biomass ratio (ABR, Eq. 4), leaf C:N ratio (LCN, Eq. 5), root C:N ratio (RCN, Eq. 6), and leaf δ^{13}C (LC, Eq. 7).

$$\text{ABR}_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon_{i,j}, \; \varepsilon_{i,j} \sim N\left(0, \sigma_{i,j}^2\right) \quad (4)$$

$$\text{LCN}_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon_j, \; \varepsilon_j \sim N\left(0, \sigma_j^2\right) \quad (5)$$

$$\text{RCN}_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j \\ + \beta_0 + \alpha_k + \varepsilon_{i,j}, \; \varepsilon_{i,j} \sim N\left(0, \sigma_{i,j}^2\right) \quad (6)$$

$$\text{LC}_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon_i, \; \varepsilon_i \sim N\left(0, \sigma^2\right) \quad (7)$$

where $\text{ABR}_{i,j}$, $\text{LCN}_{i,j}$, $\text{RCN}_{i,j}$, and $\text{LC}_{i,j}$ were the aboveground : belowground biomass ratio, leaf C:N ratio, root C:N ratio, and leaf δ^{13}C at a given levels of water (i) and nutrient (j), respectively. The parameter $\varepsilon_{i,j}$ was the residual in Eqs. 4 and 6, and assumed heterogeneity among the four combinations of water and nutrient. All the other variables are as previously defined. The model selection and assumption examination followed the same procedure as the statistical analysis above.

Effect of belowground biomass on number of sprouts.—Generalized linear model (GLM) based on Poisson distribution was used to analyze the effects of water and nutrient on number of sprouts, and there is a logarithmic link in Eq. 8 between the mean of G_i and the predictor function

$$\log(G_i) = \beta_1 \times B_i + \beta_0 + \varepsilon, \; \varepsilon \sim N\left(0, \sigma^2\right) \quad (8)$$

where G_i was the number of sprout and B_i was the belowground biomass of the ith individual plant. All the other variables are as previously defined. The model selection and assumption examination followed the same procedure as the statistical analysis above.

Maps of cogongrass presence and environmental factors

The spatial distribution data of cogongrass were obtained from EDDMapS (Early Detection and Distribution Mapping System; *available online*),[11] which is a web-based mapping system for documenting invasive species distribution. Cogongrass was first documented in the EDDMaps database in 1993 in southern Florida and continued to invade rapidly to larger areas in the southeastern United States. The locations reported to detect cogongrass in the EDDMapS were used as presence data, including 9,924 observations (Fig. 4A). To compare water and nutrient effects on distribution of cogongrass, four environmental factors were used in the analysis of species distribution model: (1) average soil water equivalents from 1948 to 2019 (mm), (2) soil available nutrients (a composite indicator of the soil characteristics relevant to soil nutrient availability, the value of which ranges from 1 to 7 for low to high nutrient availability), (3) mean annual precipitation (mm), and (4) temperature (°C) from 1981 to 2010. Note that the minimum and maximum precipitation values were also considered, but the mean precipitation had greater variable importance values than both the minimum and maximum values, hence, mean annual precipitation was used in the model, Appendix S1: Fig. S2. Source details of these data are listed in Table 1. Please note that (1) all the environmental factors were used as the long-term mean value except for the soil-available nutrients and (2) the soil-available nutrients estimate availability of soil nutrients, instead of a direct measure of soil nutrient content. To standardize the spatial data with different resolutions, we re-projected the data with uniform projection parameters and resampled the data to make the various spatial data uniform in scope and resolution. The scope is the U.S. continent (94° W to 76° W, 25° N to 36° N) and with 4-km resolution.

Species distribution model analysis

The algorithms used here need both presence and absence data; therefore, we randomly sampled three sets of pseudo-absence data within the scope of the U.S. continent based on the presence data of cogongrass. Five algorithms were used to build the models: general linear model (GLM), general additive model (GAM), generalized boosting model (GBM), maximum entropy-based model (Maxent), and random forest (RF) to ensure the results will not by biased by the choice of algorithm. The model evaluation was carried out with a repeated data-splitting procedure (cross-validation: 80% of the data were used as a training set and the remaining 20% were used as a validation set), and the procedure of cross-validation was repeated four times for each algorithm. Model accuracy was evaluated with metrics of TSS and AUC, and both suggested high accuracy of our modeling work (TSS > 0.9, AUC > 0.9). By comparing these accuracy metrics among the different choices of pseudo-absence sampling (Appendix S1: Fig. S3) and algorithm (Appendix S1: Fig. S4), we found that (1) there were

[11] www.eddmaps.org

TABLE 1. Source details of the four environmental factors used in the analysis of species distribution model.

Data	Values	Data source	Resolution	Period	Unit
Soil moisture	averaged soil moisture water height equivalents	CPC Soil Moisture	~55 km	1948–present	mm
Nutrient availability	composite indicator of the soil characteristics relevant to soil nutrient availability	FAO	~9 km	–	–
Precipitation	annual precipitation normal	PRISM University of Oregon	~4 km	1981–2010	mm
Temperature	annual mean temperature normal	PRISM University of Oregon	~4 km	1981–2010	°C

minimal differences in the accuracy among the sampling sets and (2) the model with random forest algorithm achieved the highest accuracy in the five algorithms. Therefore, outputs of the random forest model were used to make the responses curve of each environmental factor. The outputs of the five algorithms were used to calculate importance value of each environmental factor.

To predict current spatial distributions of cogongrass, we built an ensemble model that combines the information from the individual models fitted with the above algorithms. Only the algorithms with a TSS ≥ 0.8 were kept building the final ensemble model, and the ensemble option of committee averaging was used since it provided a better evaluation than the other option (weighted mean, Appendix S1: Table S1). The ensemble model predicted the current spatial distributions with the same environmental raster maps as previously used to build the individual models. The threshold value of presence–absence projections was the value maximizing the accuracy metric of TSS.

RESULTS

Total biomass and number of sprouts under the water and nutrient treatments

After seven months of growth, significantly larger total biomass (sum of above- and belowground) was accumulated in the high-water treatment than low one ($P = 0.0017$), and the similar water effect on above- and belowground biomass was also found in our study (Appendix S1: Fig. S4). No significant individual effect of nutrient treatment was found on the total biomass ($P = 0.6656$), but the interaction of water and nutrient showed a significant effect ($P = 0.0462$; Fig. 1A). The biomass difference between the low and high nutrient treatment was marginal in the low-water treatment but became larger in the high-water treatment. Moreover, the significant water effect was detected on the sprout numbers of rhizomes taken from the individuals under these treatments ($P = 0.0315$), but there were no significant differences between the nutrient treatments ($P = 0.9240$; Fig. 1B). Additionally, we found a significant positive effect of belowground biomass on the number of sprouts ($R^2 = 0.18$, $P < 0.001$), indicating that

the significant less new vegetative growth of cogongrass in the low-water treatment was associated with the lower production of belowground biomass (Fig. 1C).

Allometric and biochemical traits under the water and nutrient treatments

With the significant water effect on plant total biomass, both allometric (aboveground : belowground biomass ratio) and biochemical traits (C:N and leaf δ^{13}C) did not show significant responses to the changes in water treatment. The differences in aboveground : belowground biomass ratio, leaf C:N, root C:N, and leaf δ^{13}C between the low- and high-water treatments were all not significant (all $P > 0.05$, Fig. 2).

The water and nutrient effects on geographic distribution of cogongrass

We found clear peaks of probabilities of occurrence responding to water-related factors, e.g., soil moisture content and annual precipitation, which could be defined as optimum conditions for cogongrass (Fig. 3 B, C). The optimum conditions indicated water effect on cogongrass survival. It is important to note that once soil moisture content went beyond a certain level (~400 mm), cogongrass had a relatively constantly high probability of occurrence, until soil water level became too high (>600 mm). The response curves of soil nutrient availability showed that cogongrass has low probabilities of occurrence with less than a certain level of soil nutrient availability. However, above that level, there was a relatively constant probability of occurrence (Fig. 3A), suggesting marginal effects of soil nutrient on cogongrass survival beyond a certain threshold. Additionally, an optimum condition of temperature could be defined with the response curve of temperature (Fig. 3D). Compared with the nutrient effect, the greater water effect on cogongrass survival was suggested by the higher variable importance values of the water-related factors (average soil water equivalents and annual mean precipitation) than nutrient-related factors (Fig. 3E).

The prediction of the suitability of cogongrass occurrence, based on the ensemble model and current
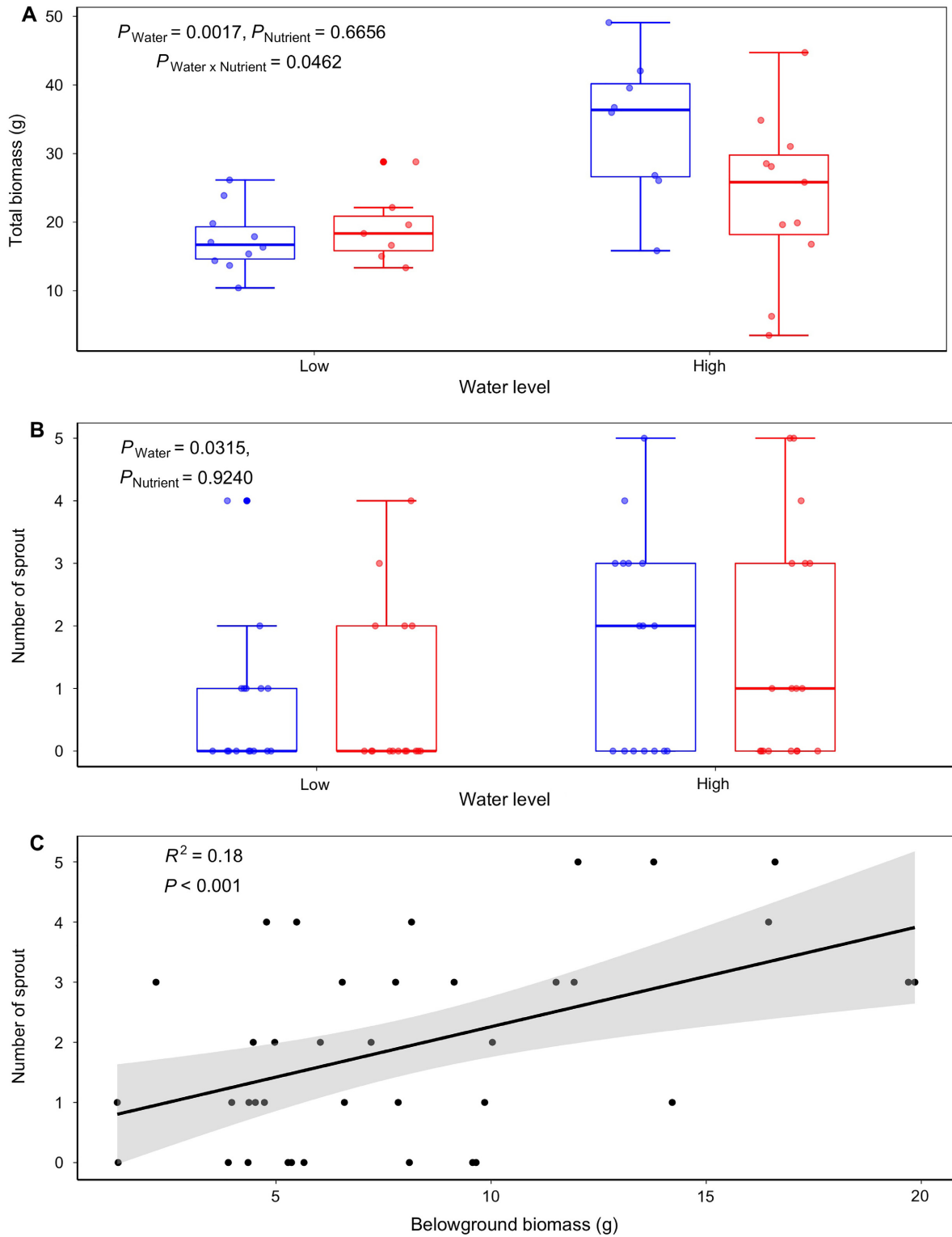
Fig. 1. Growth indices of cogongrass in the different treatments. (A) Dried total (aboveground and belowground) biomass (g); (B) Total number of sprouts in low water (low) and high water (high) treatments. Blue boxes show low nutrient treatment and red boxes show high nutrient treatment. (C) Effect of belowground biomass (g) on number of sprouts. Box plot components are midline, median value; box edges, first and third quartiles; and whiskers, one standard deviation above and below the mean of the data.
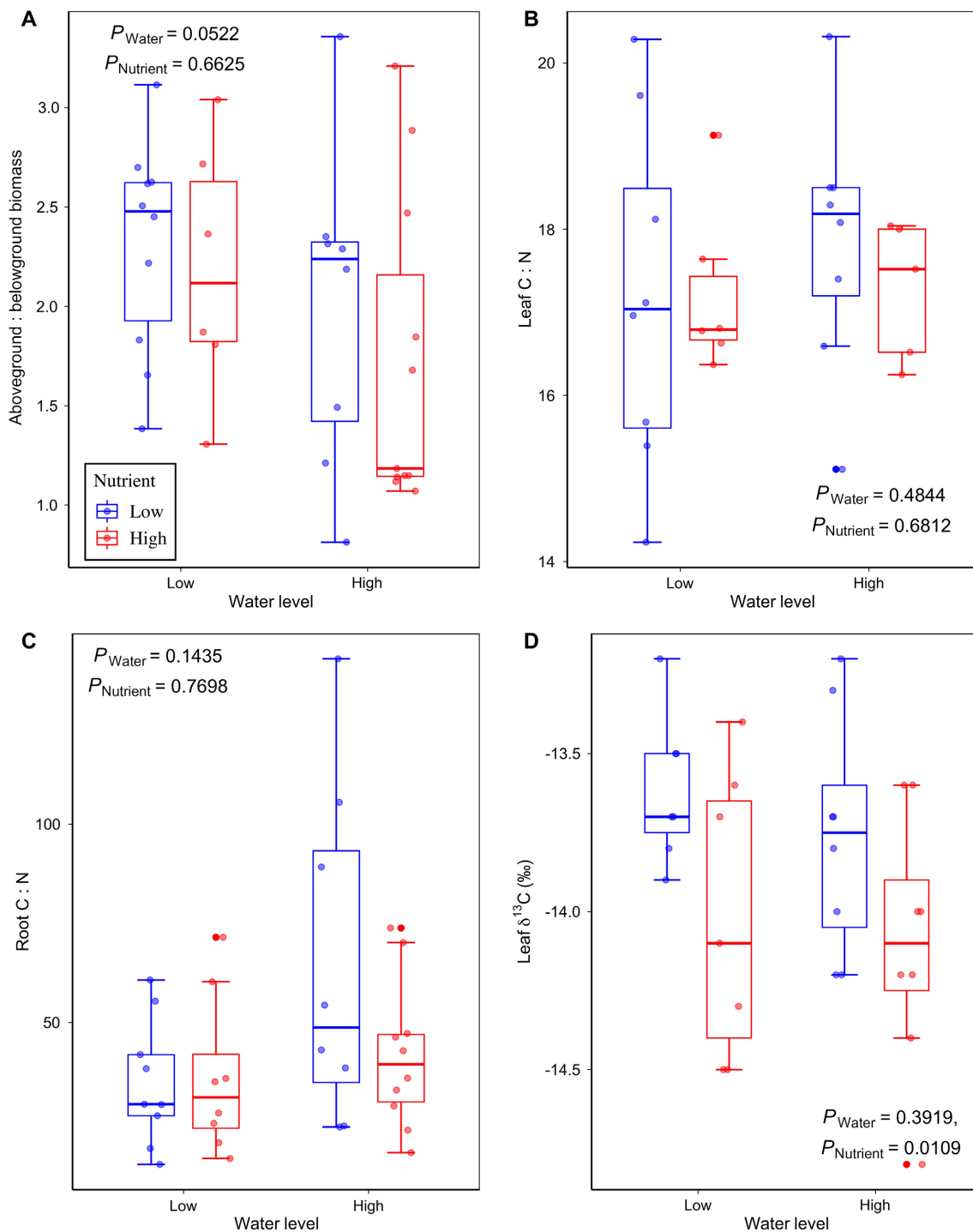
Fig. 2. Allometric and biochemical traits of cogongrass in the different treatments. (A) Above- and belowground biomass ratio; (B) leaf carbon : nitrogen ratio; (C) root carbon : nitrogen ratio; (D) leaf δ^{15}N. Blue boxes show the low nutrient treatment and red boxes show high nutrient treatment.

distributions of the four environmental factors, was shown in Fig. 4B. The projection suggested that the most suitable environment for cogongrass is in the southeastern United States where soil water content is higher together with more precipitation and warmer temperature. Additionally, cogongrass had the potential to continue invading along the eastern coast.
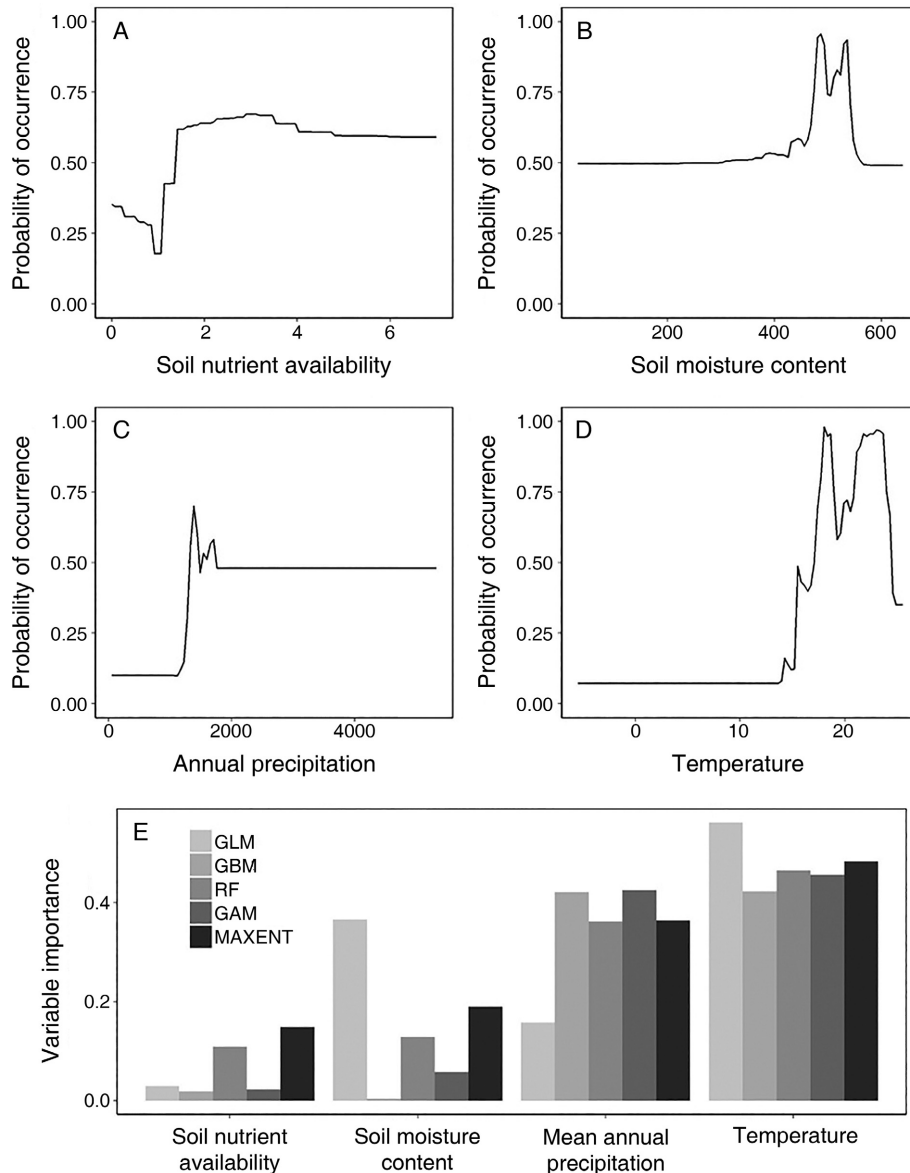
FIG. 3. (A–D) The response curves and (E) variable importance of the four environmental factors. (A) Average soil water equivalents (mm), (B) soil available nutrient (value ranges from 1 to 7 for low to high nutrient availability), (C) annual precipitation from 1981–2010 (mm), and (D) temperature from 1981–2010 (°C) under the five algorithms: general linear model (GLM), general additive model (GAM), generalized boosting model (GBM), maximum entropy-based model (Maxent), and random forest (RF).

DISCUSSION

Biomass growth of cogongrass is more sensitive to water stress than nutrient

Previous studies show that nutrient availability is one potential driver of biological invasions (Wood et al. 2006, Catford et al. 2009, Rao and Allen 2010, Dawson et al. 2012, Vallano et al. 2012, Valliere and Allen 2016a), but our study found that water availability, instead of nutrient availability, exerted a significant effect on biomass growth of a critical invasive species,

cogongrass. Furthermore, the significant biomass response to water stress was further supported by the fact that cogongrass didn't show a clear strategy to avoid the water stress, i.e., the nonsignificant differences in the allometric (aboveground : belowground biomass ratios) and biochemical (leaf C:N, root C:N, and leaf $\delta^{13}C$) traits studied. These traits can reflect different strategies of plant to avoid the water stress. For example, with increasing water stress, there could be declining aboveground : belowground biomass ratios as a drought-avoiding strategy to proportionally decrease transpiration and increase water uptake (Zhou et al.
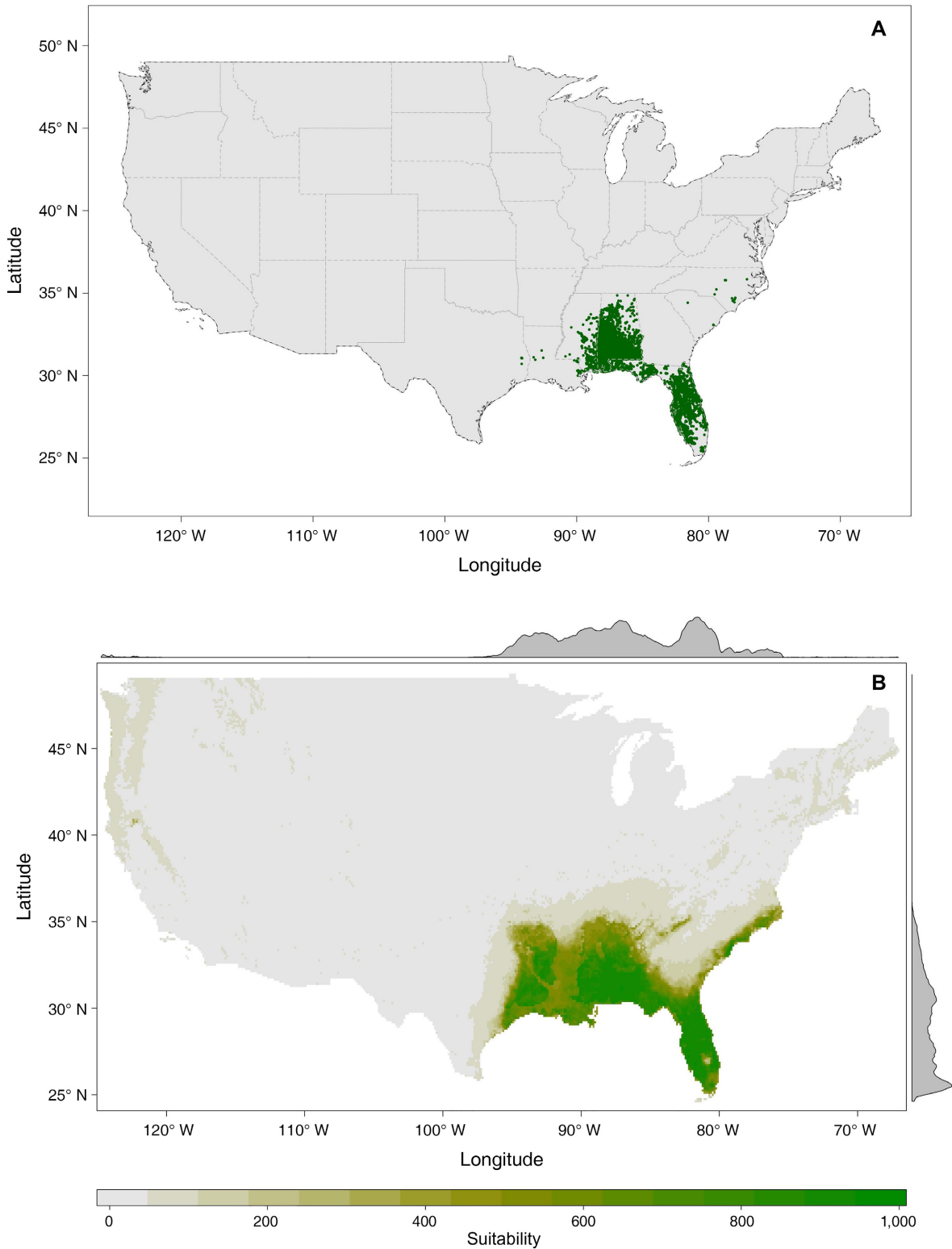
FIG. 4.   (A) The current occurrence map of cogongrass based on the EDDMapS. (B) The prediction of the suitability of cogongrass occurrence across the U.S. based on the ensemble model of the five algorithms with the four environmental factors (average soil water equivalents (mm); soil available nutrient; annual precipitation (mm) and temperature (°C)). Note that the units of projections are predicted habitat suitability (0–1) multiplied by 1,000 (thus on a 0–1,000 scale).

2018), plants with higher leaf C:N ratios show a better adaptation to water stress (Turner 1994, Urbina et al. 2015), and another strategy is to reduce plant transpiration with reduced stomatal conductance leading to higher leaf $\delta^{13}C$ values (Farquhar and Sharkey 1982). As neither of these strategies were identified in cogongrass, the observed significant biomass reduction under the low-water treatment could be associated with the lack of allometric and biochemical changes to avoid water stress. The nonsignificant nutrient effect might be attributed to luxury consumption of nutrients, i.e., absorption at a faster rate than required to sustain growth, featuring many plants particularly in nutrient-rich sites (Lambers and Oliveira 2019). The nonsignificant nutrient effect found in our study corroborates with previous studies showing that cogongrass can be well adapted to nutrient-poor soils (MacDonald 2004).

Vegetative reproduction was affected by legacy water stress

Our study found that prior stress experienced in the parental generation still played an important role in vegetative reproduction, similar to the phenomenon of "plant memory," which is an ability to access experience so that new responses incorporate previous information (Trewavas 2003). This result indicated that life history circumstances of parental generation, to some extent, affect the growth and development of the subsequent generation (Elwell et al. 2011, Wang et al. 2017). Prior water stress decreased about 40% of cogongrass total number of sprouts, whereas nutrient stress did not have that strong influence. This result agreed that invasive plants have more negative responses for growth and reproductive traits with drought impact (Facelli et al. 2005, Valliere et al. 2019). The decrease of sprout reproduction under water stress could result from the lower root biomass because seedling survivorship was positively correlated with root allocation (Lloret et al. 1999), and larger root biomass contributes to higher adaptation to various environments (Keser et al. 2015). Additionally, the lower root biomass under water stress did not support that cogongrass altered structural traits, such as allocation ratio between aboveground and belowground, in response to environmental stress.

The similar biomass allocation ratio in our study contradicts to some findings that plants could have a high degree of root plasticity to respond to environmental variation by partitioning biomass allocation (McConnaughay and Coleman 1999). Nonetheless, the constant allocation strategy of cogongrass indicated that this is a specialist species with fixed root growth strategies under drier conditions (Bongers et al. 2017, Bristiel et al. 2019). Our finding agreed with Hanslin et al. (2019) that the constant allocation ratio may be a common strategy for young perennial grass seedlings under a short period of drought stress. It is important to be aware that if cogongrass alters its biomass allocation strategy with a longer period or a greater intensity of drought still needs to be explored.

The greater water effect than nutrient effect, found in the greenhouse study, was also identified by comparing their effects on cogongrass distribution at the regional scale

With the variable importance from SDM, we found greater effects of water-related variables on cogongrass distribution at the regional scale than nutrient-related effects. Meanwhile, the greater water effect was also suggested by the growth comparison in our greenhouse study. Although the soil nutrient availability used in the model analysis is not exactly the same as the soil nutrient content in the experiment analysis, these two variables are highly related (Batjes et al. 2012). Besides explaining its current distribution, our model predicted a similar geographic directional invasion as Bradley et al. (2010b): i.e., that cogongrass will spread further north to Oklahoma and Tennessee, and east to coastal North Carolina, encroaching on numerous conservation areas. Notably, cogongrass has been found and collected in Oregon (Burrell et al. 2015). Indeed, earlier climate-change models predicted that invasive grasses would continue to be problematic and further outcompete native grasses following increased temperatures and reduced water availability (Duell et al. 2016). Additionally, cogongrass, as a C_4 grass, has been shown to ameliorate water stress in the drought treatment (Fahey et al. 2018) due to its higher water use efficiency than C_3 grass (Vogan and Sage 2011), or reduced soil surface temperature and increased humidity (Fahey et al. 2018). Our study still highlighted that continuous intense drought may inhibit nutrient uptake and further impede carbon sequestration and biomass accumulation of some invasive grass, like cogongrass. Together, it is crucial to consider the dominant forces of environmental change, the geographical location of the area invaded, and the target invasive species when understanding the relative impacts of global change on plant invasions (Bradley et al. 2010a).

Limitations

We are aware of some limitations of our species-distribution model analysis. First, although we used a standard fertilizer protocol to create a "higher nutrient condition" than the non-fertilized soil, we lacked direct measurements of final nutrient levels due to limitation by budget and human labor. It would still be helpful to measure the final nutrient level in each treatment. Additionally, we are aware that the empirical soil water content we collected had a different unit (%) than the soil moisture used in the model (mm). Hence, we cannot directly transfer laboratory data (%) to the same units as the ones used in the model to make a direct comparison between the environmental values in the experiment and in the model. Second, we only considered four environmental factors due to the limited data sources and the main focus of this

study, water and nutrient availability; other factors, such as allelopathy, land cover, radiation, topographic terrain, etc. deserve further investigation. Also, other dynamic processes, such as dispersal, were not included in the SDM, and may need to be investigated in the future. Third, we suspect the documented occurrences from EDDMapS may have considerable redundancy as the reported cogongrass populations are primarily concentrated near roadsides, paths, and recreational areas, suggesting the same cogongrass community might be reported multiple times, especially in easily accessible locations. Therefore, we have only counted each reported location once in the modeling analysis. Fourth, the quality of the EDDMapS data is not sufficient to support the statistical analysis on the contributions of the factors, such as principle component analysis. Therefore, a predictive statistical model cannot be developed at this point, and that's why the spatial correlation method was used in this study. Last but not least, our greenhouse experiment did not look at different modes of fertilization on cogongrass' fitness separately (e.g., nitrogen, phosphorous), whereas the field study has found that cogongrass is a better competitor for phosphorus than native pine–savanna plants (Brewer and Cralle 2003). Thus, these responses to different modes of soil nutrients open questions on how the estimation of habitat suitability and predictive spread of cogongrass would be altered when these responses are considered.

Conclusions

Different to prior research that nutrient enrichment plays a bigger role on facilitating biological invasions, this study highlighted the possibility that water condition may have a stronger effect on some aggressive invaders. Therefore, an important implication of this study on biological conservation is that field managers might take advantage of the negative effect of global drought on some invasive species to increase the efficiency of their controlling efforts because invasive species may become more vulnerable under drought effect.

Acknowledgments

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Data and R code (Zhang et al. 2021) to reproduce figures are available on the Dryad Digital Repository: https://doi.org/10.25338/B8SH0S.