

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

Running title: Impact of stress on invasive species

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24 **Abstract**

25 Understanding how the biological invasion is driven by environmental factors will improve
26 model prediction and advance early detection, especially in the context of accelerating
27 anthropogenic ecological changes. Although a large body of studies has examined how favorable
28 environments promote biological invasions, a more comprehensive and mechanistic
29 understanding of invasive species response to unfavorable/stressful conditions is still developing.
30 Grass invasion has been problematic across the globe; in particular, C₄ grass invaders, with high
31 drought tolerance, adaptations to high temperatures, and high water use efficiency, could become
32 more severe. Here, we conducted a rigorous microcosm experiment, with one of the most
33 damaging invasive C₄ grass - cogongrass (*Imperata cylindrica*), to explore how cogongrass
34 responds to soil water and nutrient stress. We further integrated the results of the microcosm
35 study with a species distribution model to (1) corroborate greenhouse results with field
36 observations and (2) validate the robustness of our findings at sub-continental scales. Both the
37 microcosm experiments and species distribution model agreed that cogongrass was sensitive to
38 water stress but not to nutrient stress. New vegetative growth of cogongrass continued to be
39 inhibited by the prior water stress. The significant water effect on cogongrass total biomass was
40 supported by the finding that both allometric and biochemical traits of cogongrass did not show
41 significant responses to the changes in water treatment. Contrary to the conventional wisdom that
42 nutrient enrichment plays a bigger role in facilitating biological invasions, this study highlighted
43 the possibility that water conditions may have a more substantial effect on some aggressive
44 invaders. Therefore, an important implication of this study on biological conservation is that
45 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: Cogongrass, Water stress, Nutrient stress, Biological invasion, C₄ grass, Microcosm experiment, Species distribution model

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, Pimentel et al. 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 content, thus leading to positive feedback that attracts more invasions (Ehrenfeld 2003, 2010). Despite global nitrogen deposition and drought are increasing environmental problems (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 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 root, 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 ones 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, Sardans and Peñuelas 2012, Urbina et al. 2015). Additionally, changes in reproduction traits represent another surviving strategy across generations, i.e., to sustain the growth of future generations instead of current one, stressed plants could allocate more biomass to reproduction and maintain its quality (e.g., maintain the number of re-sprouts in next growing season). The aforementioned changes in plant traits may make different contributions to the 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 gaining 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, Saveriaid 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 study to date has 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 Federal Noxious Weed in the U.S. (Lowe et al. 2000). Specifically, we used ¹⁵N 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 below-ground 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 consistent with 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 an aggressive, pernicious, rhizomatous perennial C₄ grass (Holzmueller and Jose 2011), which spreads mainly via seeds and rhizomes (McConnaughay and Coleman 1999, MacDonald 2009). Due to its C₄ 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 C₃ invaders. Since its initial introduction to the U.S., cogongrass has expanded its range in the Southeastern U.S. 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 & Nematology Department greenhouse of at the University of Florida Gainesville, FL and relocated to a greenhouse at the Institute of Food and Agricultural Sciences (IFAS), University of Florida, Davie, FL. 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 south-eastern 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, FL. Greenhouse temperatures were maintained at 25–30 °C, corresponding roughly to ambient temperatures from September to March in the region. Single- cogongrass rhizome fragments ($\approx$ 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 $\times$ 20 cm lower diameter $\times$ 23 cm height) filled with commercial potting mix (Fafard® Professional Growing Mix, Sun Gro® Horticulture Canada Ltd., Agawam, MA). Note that the potting soil we used here contains Canadian Sphagnum peat moss, bark, perlite, 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

158 saturated for one month and only the pots with successful rhizome germination were used for
159 later experiments.

160 Our experiment was a full factorial design consisting of two factors: water (low and high)
161 and nutrient (low and high) frequencies. In the low water treatment, water was applied to the soil
162 surface until saturation every month (soil moisture $\approx 34 \pm 7\%$), and in the high water
163 treatment, water was provided every two weeks (soil moisture $\approx 90 \pm 6\%$). The watering
164 frequency was modified according to the watering periods used in Webster and Grey (2008) to
165 have a close representation of the weather in Florida, which also resulted in similar soil water
166 contents that Burns (2004) used in her study. Indeed, a further lower water level could be used to
167 mimic a stronger drought (Burns 2004, Alba et al. 2019), our watering period was designed
168 based on a comprehensive consideration on watering period and soil water content to have a
169 close representation of the weather in Florida, which also aimed to mimic meteorological
170 drought to ultimately show vegetation physiological drought response. The low nutrient
171 treatment received no additional nutrient fertilizer across the entire experiment and high nutrient
172 treatment received constant nutrient fertilizer every two weeks. Fertilizer was purchased from
173 General Hydroponics (genhydro Inc, CA, USA). The fertilizer was dispensed into each pot
174 according to the manufacturer's recommendations (Total Nitrogen: 0.009%; P_2O_5 : 0.007%; K_2O :
175 0.014%). Each treatment was replicated 11 times (total of 44 pots) (experimental setup is shown
176 in Appendix S1: Fig. S1A and four randomly selected pots from each treatment are shown in
177 Appendix S1: Fig. S1B). The total 44 pots were placed in a randomized complete block design in
178 the greenhouse. The duration of the experiment was seven months from September 2018 to
179 March 2019.

180 **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), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment, we first oven-dried samples at 60 °C for 48 h to constant weight 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 mm × 8 mm; Elementar Americas, Mt. Laurel, NJ, 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 was measured as a weight percentage of total foliar C and N relative to total leaf dry mass. Isotopic compositions, as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, were expressed as:

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

where R_{sample} is the C or N stable isotope ratio (i.e., $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$) 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 (± 1 standard deviation) and the precision of the C and N isotopic analysis was $\pm 0.1\text{‰}$ (± 1 standard deviation).

We harvested all the plants in the beginning of April 2019 and separated the above- and below-ground 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), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment. We used the same protocol as we performed with the foliage as described earlier. To determine if the vegetative reproduction of the same generation was affected by prior water and nutrient conditions, three randomly selected rhizome fragments (≈ 15 cm in length with at least four nodes) were cut in each pot and replanted horizontally into a new pot (25 cm upper diameter $\times$ 20 cm lower diameter $\times$ 23 cm height) filled with the same commercial potting mix (Fafard[®] Professional Growing Mix, Sun Gro[®] Horticulture Canada Ltd., Agawam, MA). 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.

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

Data analysis

1. 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 sprout, and there is a logarithmic link in the Eq.3 between the mean of $G_{i,j}$ and the predictor function.

$$TB_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_{3,i,j} \times W_i \times N_j + \beta_0 + \alpha_k + \varepsilon_i, \varepsilon_i \sim N(0, \sigma_i^2) \dots \text{Eq. 2}$$

$$\log(G_{i,j}) = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon, \varepsilon \sim N(0, \sigma^2) \dots \text{Eq. 3}$$

where $TB_{i,j}$ and $G_{i,j}$ were the total biomass and number of sprout at a given level of water (i) and nutrient (j), respectively. $\beta_{1,i}$ was the coefficient of W_i (the i^{th} level of fixed water factor). $\beta_{2,j}$ was the coefficient of N_j (the j^{th} 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 k^{th} table. ε_i and ε were the residual in the Eq. 2 and 3, respectively. 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 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 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 by R program (Kuhn et al. 2020) and the "nlme" package (Pinheiro et al. 2012).

2. 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: Above- :

Belowground biomass ratio (ABR, Eq. 4), leaf carbon (C) : nitrogen (N) ratio (LCN, Eq. 5), root C : N ratio (RCN, Eq. 6), and leaf $\delta^{13}\text{C}$ (LC, Eq. 7).

$$ABR_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon_{i,j}, \varepsilon_{i,j} \sim N(0, \sigma_{i,j}^2) \dots \text{Eq. 4}$$

$$LCN_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon_j, \varepsilon_j \sim N(0, \sigma_j^2) \dots \text{Eq. 5}$$

$$RCN_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \alpha_k + \varepsilon_{i,j}, \varepsilon_{i,j} \sim N(0, \sigma_{i,j}^2) \dots \text{Eq. 6}$$

$$LC_{i,j} = \beta_{1,i} \times W_i + \beta_{2,j} \times N_j + \beta_0 + \varepsilon_i, \varepsilon_i \sim N(0, \sigma^2) \dots \text{Eq. 7}$$

where $ABR_{i,j}$, $LCN_{i,j}$, $RCN_{i,j}$, and $LC_{i,j}$ were the Above- : Belowground biomass ratio, leaf carbon (C) : nitrogen (N) ratio, root C : N ratio, and leaf $\delta^{13}\text{C}$ at a given levels of water (i) and nutrient (j), respectively. $\varepsilon_{i,j}$ was the residual in the Eq. 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 in the statistical analysis above.

3. 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 the Eq. 8 between the mean of G_i and the predictor function.

$$\log(G_i) = \beta_1 \times B_i + \beta_0 + \varepsilon, \varepsilon \sim N(0, \sigma^2) \dots \text{Eq. 8}$$

Where G_i was the number of sprout and B_i was the belowground biomass of the i^{th} individual plant. All the other variables are as previously defined. The model selection and assumption examination followed the same procedure in the statistical analysis above.

Maps of Cogongrass presence and environmental factors

The spatial distribution data of cogongrass was obtained from EDDMapS (Early Detection & Distribution Mapping System) (www.eddmaps.org), 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 U.S. The locations reported to detect cogongrass in the EDDMapS were used as presence data, including 9924 observations. 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 - 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) annual mean precipitation from 1981 – 2010 (mm) and mean temperature from 1981 - 2010 (°C). 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; (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 re-sampled the data to make the various spatial data uniform in scope and resolution. The scope is the U.S. continent (W94, W76, N25, N36) 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. Four algorithms were used to build the models: general linear model (GLM), general additive model (GAM), generalized boosting model (GBM), and random forest (RF). 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). This entire procedure was repeated four times. Model accuracy was evaluated with metrics of TSS and AUC that suggest high accuracy of our modeling work ($TSS > 0.9$, $AUC > 0.9$). By comparing these accuracy metrics among the different choices of pseudo-absences sampling (Appendix S1: Fig. S2) and algorithm (Appendix S1: Fig. S3), we found that there were minimal differences in the accuracy among the sampling sets and the model with random forest algorithm achieved the highest accuracy in the four algorithms. Therefore, outputs of the random forest model were used to make the responses curve of each environmental factor. The outputs of the four 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 four algorithms. Only the algorithms with a TSS greater than or equal to 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

1. 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 below-ground) 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). For example, 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).

2. Allometric and biochemical traits under the water and nutrient treatments

With the significant water effect on plant total biomass, both allometric (above- : belowground biomass ratio) and biochemical traits (C : N and leaf $\delta^{13}\text{C}$) did not show significant responses to the changes in water treatment. For example, the differences in above- : belowground biomass ratio, leaf C : N, root C : N, and leaf $\delta^{13}\text{C}$ between the low and high water treatments were all not significant ($p = 0.0522$, 0.4844 , 0.1435 , and 0.3919 , respectively, Fig. 2).

3. 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 A and C). The optimum conditions indicated the greater water effect on cogongrass survival. Differently, 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 the level, there was a relatively constant probability of

occurrence (Fig. 3B), 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. 3 D). Compared with the nutrient effect, the greater water effect on cogongrass survival was further suggested by the higher variable importance values of the water-related factors than nutrient factors (Fig. 3E). Based on the modeling results, the greater water effect was consistent to our findings from the experiments (Fig. 1).

The prediction of the suitability of cogongrass occurrence, based on the ensemble model and current distributions of the four environmental factors, was shown in the Fig. 4. The projection suggested that the most suitable environment of cogongrass is in the southeastern U.S. 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.

Discussion

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

Although previous studies showing 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), our study found that water availability, instead of nutrient, exerted a significant effect on biomass growth of a critical invasive species, cogongrass, which may further modulate the effects of nutrients. 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 non-significant differences in the allometric (above- : belowground biomass ratios) and biochemical traits (leaf C : N, root C : N, and leaf $\delta^{13}\text{C}$) studied. These traits can reflect different strategies of plant to avoid the water stress. For

example, with increasing water stress, there could be declining above- : belowground biomass ratios as a drought-avoiding strategy to proportionally decrease transpiration and increase water uptake (Zhou et al. 2018) and plants with higher leaf C:N ratios show a better adaptation to water stress (Turner 1994, Sardans and Peñuelas 2012, Urbina et al. 2015). Another strategy is to reduce plant transpiration by decreasing stomatal conductance, leading to higher leaf $\delta^{13}\text{C}$ values (Farquhar and Sharkey 1982). However, these strategies were not identified from cogongrass, potentially contributing to the significant biomass reduction under the low water treatment. The non-significant 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 non-significant nutrient effect found in our study corroborates with previous studies showing that cogongrass can remain competitive under nutrient limitation (Prince et al. 2018).

2. 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 above and below ground, 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.

3. Consistent pattern of cogongrass response to various environmental conditions at multiple spatial scales

Consistent with our greenhouse experimental results, the water conditions showed more effects on the spatial distribution of cogongrass than the nutrient conditions, suggested with the higher variable importance of soil water and precipitation than soil nutrient availability. Although the soil nutrient availability used in the model analysis is not exactly 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. More importantly, cogongrass has been found and collected in Oregon (Burrell et al. 2015), suggesting that our prediction based on the arithmetic mean is more accurate than the one based on the geometric mean. 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 C₄ grass, has shown to ameliorate water stress in the drought treatment (Fahey et al. 2018) due to its general higher water use efficiency than C₃ grass (Vogan and Sage 2011), or the 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).

4. 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 unit as the ones used in the model to make direct comparison between the environmental values in the experiment and in the model. Secondly, we

only considered four environmental factors due to the limited data sources and the main focus of this study was 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 investigate 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. Forth, 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 fertilizer on cogongrass' fitness separately (e.g., nitrogen, phosphorous), whereas, 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

Contrary 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, in particular those <<Add traits that enable strong

influences of water on these aggressive species>>. 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.

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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	~55km	1948-	mm
Nutrient Availability	composite indicator of the soil characteristics relevant to soil nutrient availability	FAO	~9km	-	-
Precipitation	Annual precipitation normal	PRISM University of Oregon	~4km	1981- 2010	mm
Temperature	Annual mean temperature normal	PRISM University of Oregon	~4km	1981- 2010	°C

Figures

Figure 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 box: low nutrient treatment and red box: high nutrient treatment. C: Effect of belowground biomass (g) on number of sprouts.

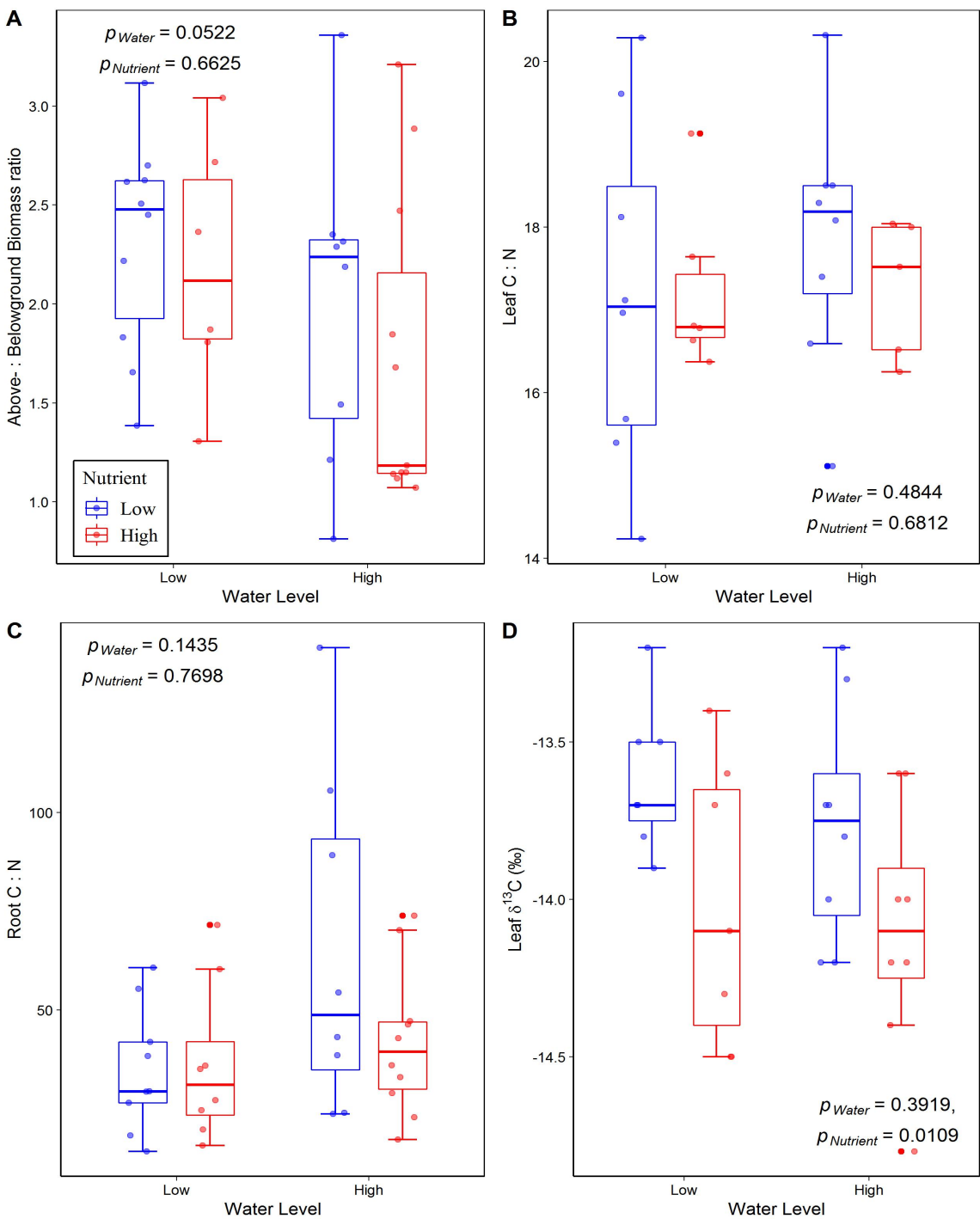
Figure 2. Allometric and biochemical traits of cogongrass in the different treatments. A: Above- and Belowground biomass ratio; B: Leaf carbon (C) : nitrogen (N) ratio; C: Root carbon (C) : nitrogen (N) ratio; D: leaf $\delta^{15}\text{N}$. Blue box: low nutrient treatment, and red box: high nutrient treatment.

Figure 3. The response curves (A - D) and variable importances (E) 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 ($^{\circ}\text{C}$).

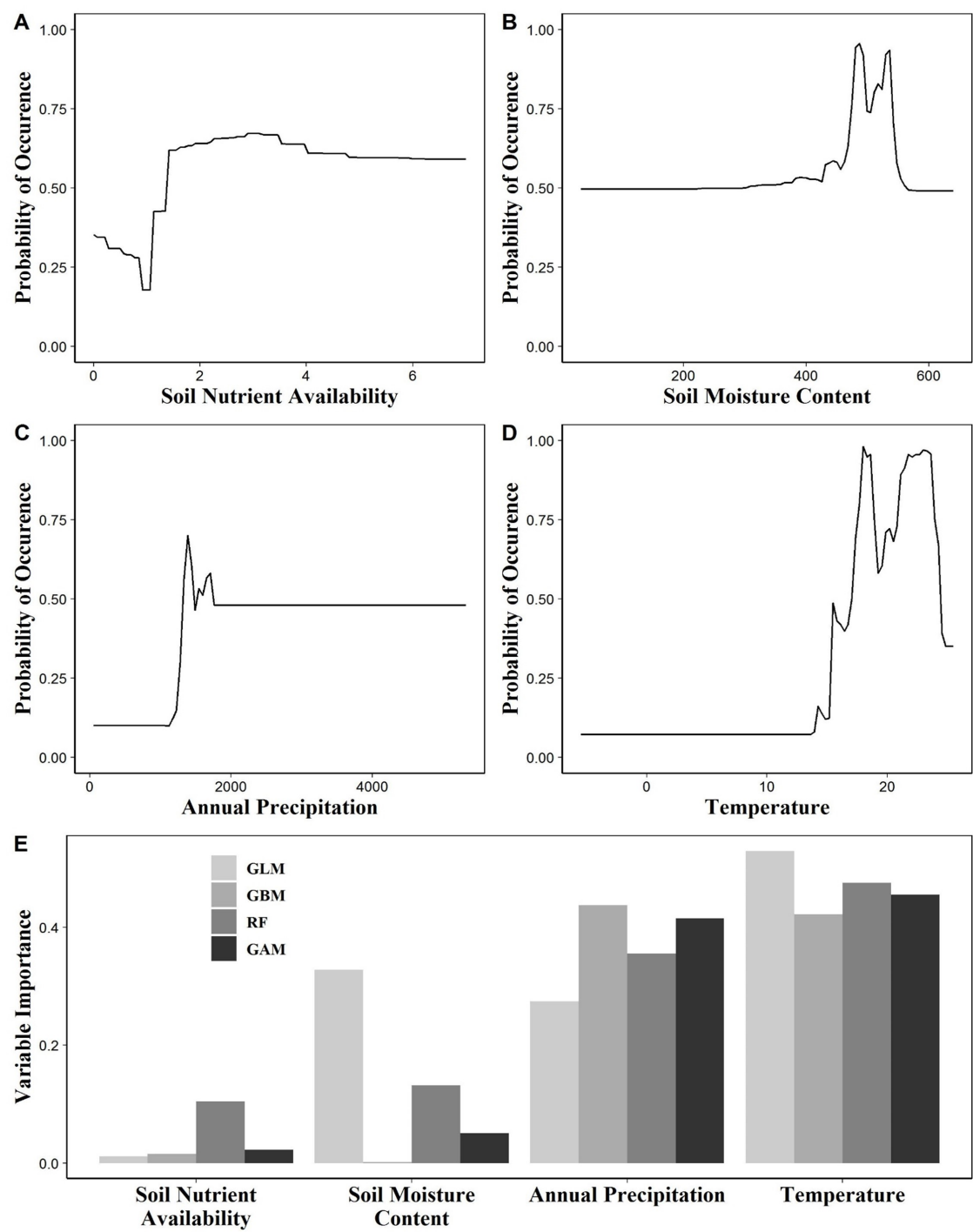
Figure 4. The prediction of the suitability of cogongrass occurrence across the U.S. continent based on the ensemble model of the four algorithms with the four environmental factors (average soil water equivalents (mm); soil available nutrient; annual precipitation (mm) and temperature ($^{\circ}\text{C}$)). Note that the units of projections are predicted habitat suitability (0~1) multiplied by 1000 (thus on a 0~1000 scale).



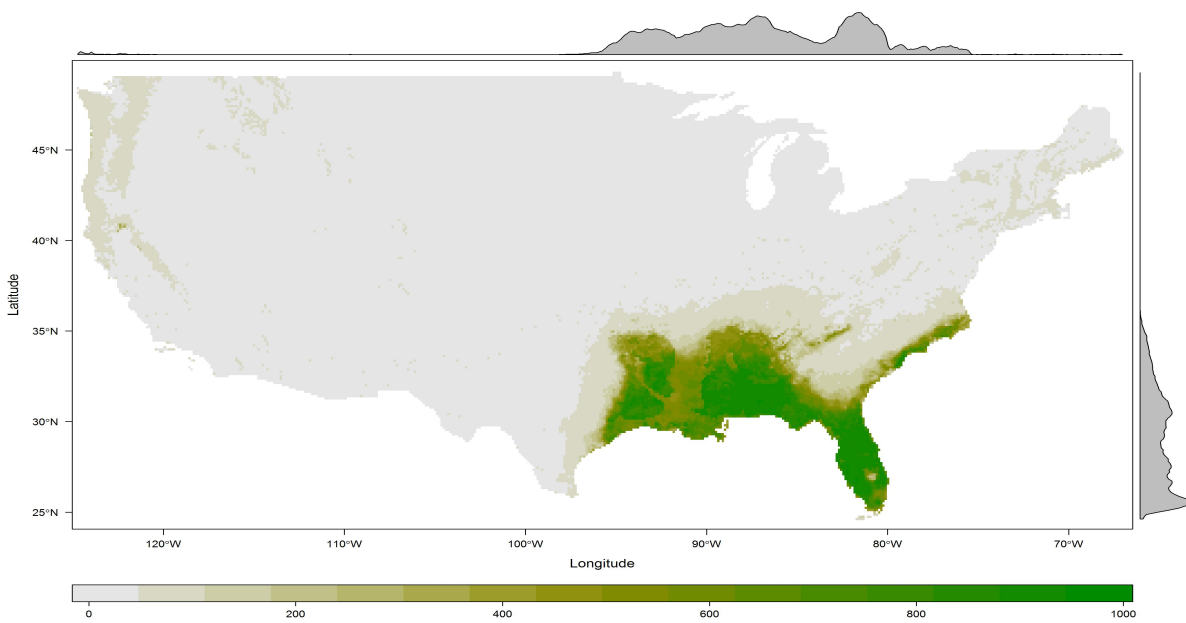
723 Figure 2



728 Figure 3



732 Figure 4



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