EFFECTS OF LATITUDE ON THE COMPETITIVE ABILITY OF NATIVE AND INVASIVE GENOTYPES OF *PHRAGMITES AUSTRALIS*

A Thesis Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Masters of Science in The Department of Biological Sciences

By

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Contrary to popular belief, fish and family are not the same. Without my family, I would not be whole. To my grandpa and grandma, who have always loved and supported me unconditionally, a special thanks. Without them and their lessons on hard work, humility, and strength I truly would not be where I am today. To my extended family in Michigan, thanks for always looking out for me and the survival packages on my birthday and the holidays.

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ABSTRACT

One commonly cited mechanism for the success of invasive species is their superior competitive ability relative to that of native species. -Although xx% (x of 25) of the empirical studies ~~research~~ ~~generally~~ supports the prediction that the strength of competition for native species increases with latitude, no studies to date have compared the competitive ability of native and co-occurring invasive species across a broad latitudinal range. -In a greenhouse, I investigated whether the competitive ability of North American native and European invasive ~~haplotypes~~ haplotypes of *Phragmites australis* vary ~~in parallel~~ with latitude. Another widespread, non-indigenous haplotype, the Gulf Coast haplotype, was also included for assessment of competitive ability only. ~~The experiment involved 8 populations of the invasive haplotype (spanning a latitudinal range of 17°), 3 populations of the native haplotype (a range of 4.5°), and 2 populations of the Gulf Coast haplotype.~~ Competitive ability of each haplotype was evaluated against a standardized plant species, *Spartina alterniflora*, which is a common co-inhabitant of coastal marshes. ~~This study provides the first evidence that native and invasive species (or haplotypes) exhibit non-parallel gradients in competitive ability (i.e., a latitude-by-haplotype interaction in terms of competitive ability).~~ The competitive ability (measured in terms of the proportional reduction in biomass of plants grown in the presence and absence of a potential competitor) of native haplotypes decreased with increasing latitude, whereas the competitive ability of invasive haplotypes showed no relationship with latitude. -This study provide~~s~~d the first evidence that native and invasive species (or haplotypes) exhibit non-parallel gradients in competitive ability ~~(i.e., a latitude-by-haplotype interaction in terms of competitive ability).~~ -Overall, t~~T~~he invasive haplotype was competitively superior to the native haplotype - biomass production of *S. alterniflora* was 19% lower when grown with the former than the latter

Commented [JTC1]: Might as well incorporate your lit review in the Abstract.

haplotype. Moreover, in the presence of an interspecific competitor, the invasive haplotype produced 45% more aboveground biomass and 50% more belowground biomass than the native haplotype. -Results also indicated that the ~~introduced~~ Gulf Coast haplotype was not significantly different from either the native or invasive haplotypes in terms of competitive ability. -Because the invasive haplotype appeared to have the greatest competitive advantage over the natives at northern latitudes, it may be more successful in this region of its invaded range. -The results from this research indicate that novel and important findings are possible when the mechanisms concerning invasion success, such as biotic resistance and competition, are examined from a biogeographical perspective.

INTRODUCTION

Invasive species, ~~(i.e.,~~ introduced species that generate self-propagating populations capable of widespread dispersal (Richardson et al. 2000)~~)~~, are well known for the negative impacts they have on community composition and function (Vitousek et al. 1996; Wilcove et al. 1998; Mack et al. 2000; Simberloff et al. 2013; Bezemer et al. 2014). ~~As a group of organisms,~~ ~~i~~Invasive species comprise a majority of the most widespread plant species in North America (Stohlgren et al. 2011), and are an important part of human mediated global change (Vitousek et al. 1997). An important line of inquiry is why do some exotic species become "invasive" ~~whereas~~ but others fail to establish or establish but do not spread or negatively affect resident species (i.e. naturalized species)?~~.~~

One commonly cited mechanism for the success or failure of an invasive species is the competitive ability of the invasive species relative to that of co-occurring native species (Bakker and Wilson 2001; Vila and Weiner 2004). In a review of 36 experimental studies, Vila and Weiner (2004) found that in 26 of the studies, native plant species were more negatively affected by competition with invasive species than by competition with themselves. Additionally, Blank (2010) and French (2012) showed that invasive plant species cause a greater reduction in native plant species shoot growth, root growth, plant tissue nutrient levels, and soil nutrient availability than vice versa. It has been argued that greater competitive ability in invasive versus native species is the result of the size differential between the two species; i.e., invasive species tend to be larger and outcompete smaller native species (Dostal 2011). Although the majority of evidence supports the view that invasive species are better competitors than native species (e.g., Vila and Weiner 2004), a number of studies have shown that native species are the better competitors (Corbin and D'Antonio 2004). In these cases, native species may act as bulwarks against the establishment and spread of invasive species (i.e. biotic resistance hypothesis; (Elton 1958; Levine et al. 2004)).

One possible explanation for the inconsistent findings is that strength of competitive ability between native and invasive species may vary in different ways over broad geographic or continent-wide spatial scales (i.e., they may exhibit non-parallel gradients in competitive ability). L~~ Most notably, in temperate regions as opposed to tropical regions, invasive species are found in greater numbers at lower latitudes and demonstrate larger geographical ranges at higher latitudes (Sax 2001). It is possible that latitudinal variation in abiotic factors, such as resource availability, or biotic factors, such as the competitors present, can generate such a phenomenon (Sax 2001). For native species a pattern of higher diversity in tropical regions versus temperate regions is observed. Furthermore, l~~ongstanding ~~competing~~ theories predict that competition intensity in resident native species can either decrease or increase with latitude, as a function of both community composition and resource availability (Dobzshanky 1950; Pianka 1966; Huston 1979; Schemske et al. 2009). For example, if a shared resource between two native species decreases with increasing latitude, then competitive intensity and ability is expected to increase with latitude. Native species should adapt in response to the availability of these resources. ~~Therefore, native species that are coevolved respond in parallel to latitudinal gradients in abiotic and biotic factors. For example, if a shared resource between two native species decreases with increasing latitude, then competitive intensity and ability is expected to increase with latitude.~~

Based on a literature search using Web-of-Knowledge (19xx – 2013; key words: xxxxx), 25 studies have examined whether competitive ability varies with latitude (Table 1). Of those studies, the vast majority (88%; 22 of 25) provided evidence that competitive ability of native species varied with latitude. X% and Y% of the studies showed that competitive ability increased or decreased with latitude, respectively. For plants only, X of Y studies supported the prevailing prediction that competitive ability is greater at lower latitudes. ~~In their study of mesic forest tree populations Jordan and Murphy (1978) found that competitive ability for light in northern tree populations was higher than in southern tree populations. However, a majority of studies concerning competitive ability with plant biomass as a proxy have shown increased competitive ability at lower latitudes (Table 1). Of 25 species in which putative competitive traits were studied, no significant latitudinal effect was only found in 3 species whereas in the remaining 22 species the direction of the latitudinal cline in competitive ability varied with species (Table 1).~~To date, no studies have examined latitudinal gradients for invasive species.

Commented [JTC2]: Is that correct? You may want to provide an interesting plant example that supports this prediction.

Table 2. Studies that examined the relationship between latitude and ~~Literature review tables of all species in which latitudinal clines in~~ competitive ability ~~have been examined~~.

Our expectation is that ~~However,~~ invasive species may have spread rapidly in their new region and may not have had sufficient time to evolve a latitudinal cline~~s~~ in competitive ability that parallels potential native competitors. ~~As such, the relative competitive abilities of native and invasive species may not parallel each other along a latitudinal gradient.~~ One possible scenario ~~in which competitive abilities may differ at some latitudes, be equivalent at others, and exhibit reversals in rankings at other latitudes~~ is presented in Fig. 1. Non-parallel gradients in competitive ability between native and invasive species may create a situation where, in some areas, the native species outcompete invasive species, which would support the notion of biotic resistance (REFERENCES; Fig. 1, hatched area), whereas in other areas, the invasive species is the better competitor (REFERNCES; Fig. 1, grey area). ~~If competitive ability of native species varies with latitude~~In the case of non-parallel gradients, ~~then~~ the difference in competitive ability between native and invasive species may depend on three factors: 1) the latitude from which the invasive species originates; 2) the speed and direction at which the invasion proceeds; and 3) the time since arrival or rate at which the invasive species evolves in response to the latitudinal gradient. -Although differences in competitive ability between native and invasive plants and the effect of latitude on competitive ability are important, such a combined direct biogeographic approach has not been explored (Schemske et al. 2009). ~~Non-parallel gradients in competitive ability between native and invasive species may result in areas where native species outcompete invasive species and vice versa.~~

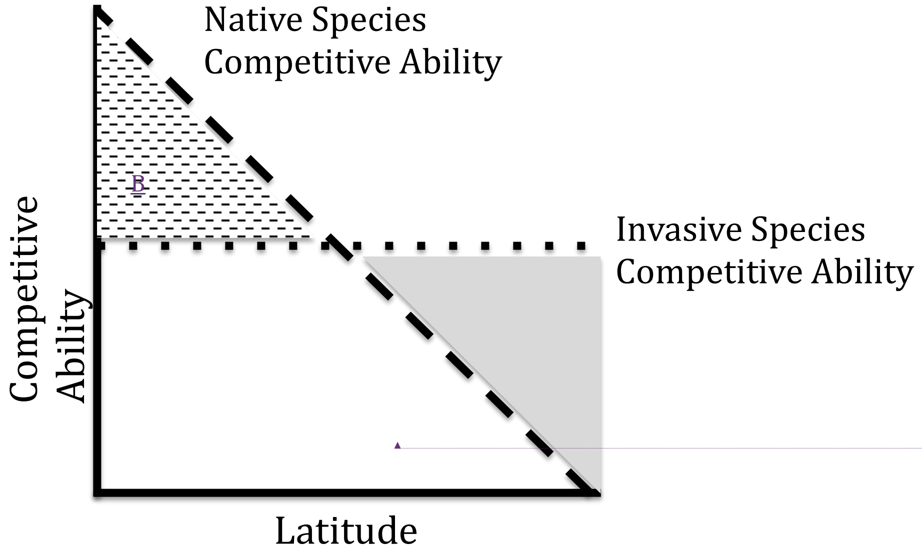

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Figure 1. ~~Theoretical~~ Hypothetical differences in competitive ability ~~over~~ with respect to latitude between native (solid line) and invasive species (dashed line) ~~(from Bezemer et al. 2014)~~. Hatched and sh~~ The dotted line indicates the competitive ability of invasive species, whereas the dashed line indicates the competitive ability of native species. Sh~~aded areas indicate~~s~~ regions where the native species has higher and lower competitive ability, respectively, than the invasive species~~of either higher (top) or lower (lower) biotic resistance that occur in the absence of parallel clines in competitive ability between native and invasive species over latitude~~.

~~If competitive ability of native species varies with latitude, then the difference in competitive ability between native and invasive species may depend on three factors: 1) the latitude from which the invasive species originates; 2) the speed and direction at which the invasion proceeds; and 3) the time since arrival or rate at which the invasive species evolves in response to the~~

~~latitudinal gradient. Although differences in competitive ability between native and invasive plants and the effect of latitude on competitive ability are important, such a combined direct biogeographic approach has not been explored (Schemske et al. 2009). Non-parallel gradients in competitive ability between native and invasive species may result in areas where native species outcompete invasive species and vice versa.~~

The objective of this study was to determine whether the relative competitive abilities of co-occurring native and invasive plants vary with latitude and in parallel with each other. For this study, I chose common reed, *Phragmites australis* (Poaceae), which is unique in that both native and Eurasian invasive haplotypes (based on chloroplast DNA analysis) coexist together in North America over a broad latitudinal range (Saltonstall 2002). One clear advantage of using conspecific plants is that there is an inherent phylogenetic control when making comparisons between natives and invasives (i.e., provenance or source of plant material), and among latitudes. Specifically, I test the predictions that: 1) the invasive haplotype of *P.australis* is larger and has greater competitive ability than native haplotypes when tested against a standardized native wetland species; 2) the competitive ability of the native haplotype increases with increasing latitude; and 3) the invasive haplotype ~~does not~~ exhibits ~~a~~ no latitudinal gradient in competitive ability.

Commented [JTC3]: ok. Is the predicted (based on literature or Table 1) outcome an increase or decrease in competitive ability with latitude? Fig 1 shows the opposite of your stated pattern.

MATERIALS AND METHODS

Study Species

Phragmites australis~~, the common reed (Poaceae)~~, has a cosmopolitan distribution with a northern distribution limit of Norway and southern distribution limit of extreme South America, and is commonly found in estuaries, the borders of inland water bodies, and coastal wetlands (Haslam 1972). *P. australis* typically forms dense monospecific patches 2-5m in height (Hara et al. 1993). Growth of *P. australis* varies in response to latitude with the production of taller stems and thicker rhizomes at lower latitudes and higher shoot length growth rate and earlier flowering times at higher latitudes. These growth patterns suggest~~; suggesting~~ possible size-~~-~~based variation~~s~~ in competitive ability with latitude (Clevering et al. 2001). As invasive *P. australis* has increased its coverage, other species such as the endangered endemic *Eriocaulon carsonii* and common forbs such as *Atriplex patula var. hastata* and *Solidago sempervirens* have declined or disappeared (Minchinton et al. 2006; Davies et al. 2010).

Once common throughout the United States and southern Canadian Provinces, endemic native populations of *P. australis* have become relatively rare, possibly because they have been competitively displaced by European invasive haplotypes (Saltonstall 2002). The invasive haplotype of *P. australis* (M) has attained a broad distribution over much of North America, extending beyond the range previously occupied by native populations. Based on an analysis of modern day samples and herbarium specimens dating as far back as the mid-1800s, the invasive haplotype of *P. australis* has experienced a rapid increase in distribution since 1910 from its likely introduction point along the Atlantic coast. ~~Population~~Specimens of the invasive haplotype in North America prior to 1910 ~~was only~~constituted 6% of the herbarium records, but by 1960 had increased to 62% (Saltonstall 2002). Through the use of both morphological and genetic characteristics, native and invasive populations of *P. australis* can be distinguished (Saltonstall 2002; Meadows and Saltonstall 2007). In comparison to the invasive haplotype, the native haplotypes senesce earlier, have a different culm color (maroon or bright yellow), may possess black culm spots, and drop their leaf sheaths and leaves after senescence (Meadows and

Saltonstall 2007). By utilizing two specific noncoding chloroplast regions and 10 microsatellite loci, three distinct *P. australis* haplotype groups have been found in North America: Native (haplotypes A-H, S, Z, AA-AC), Invasive (haplotype M and its M1 variant "Delta", L1), and Gulf Coast (haplotype I) (Saltonstall 2003; Hauber et al. 2011; Lambertini et al. 2012, Meyerson and Cronin 2013).

Commented [JTC4]: there are other haplotypes as well.

Although both the native and invasive haplotypes of *P. australis* are genetically the same species, the invasive haplotype is generally able to tolerate a broader range of abiotic conditions (tolerance to high salinity), and possesses traits that are thought to confer greater competitive ability than the native haplotypes (Bart and Hartman 2000; Burdick and Konisky 2003; Vasquez et al. 2005; Ba et al. 2006; Kettenring and Mock 2012). For example, under a broad range of abiotic conditions (e.g., nutrient availability and salinity), the invasive haplotype has a higher relative growth rate, more shoot tissue per gram of rhizome tissue, taller stems with a greater number of nodes, 50% larger leaves, and a higher number of shoots produced than native haplotypes (League et al. 2006; Saltonstall and Stevenson 2007; Vasquez et al. 2005).

Experimental Approach

To ~~accurately~~ assess differences in competitive ability between native and invasive haplotypes of *P. australis*, I used the methodology outlined by Vila and Weiner (2004) ~~was used~~. Here, the strength of competition of native and invasive haplotypes against a common target species, *Spartina alterniflora* (Poaceae), was assayed in a greenhouse environment. Because there was no flowering in the experimental pots due to the short duration of the experiment, aboveground and belowground biomass were used as the best measures of plant fitness. ~~The strength of~~

~~competition was measured in terms of the impact of one species on the aboveground and belowground biomass production of the other species.~~ Based on these biomass measures, I computed ~~In addition to measurements of biomass,~~ the relative competition intensity index (RCI), which ~~measures~~ is the proportional decrease in ~~the target plant's~~ biomass production of *S. alterniflora* in response to the presence of one or the other haplotype of *P. australis* ~~due to competition with either the native or invasive haplotype of *P. australis* was also computed based on the aboveground biomass of *S. alterniflora*~~ (Belcher et al. 1995). Separate measures were obtained for aboveground and belowground biomass. ~~Similarly, t~~The competitive effect of the ~~*target plant*~~*S. alterniflora* on *P. australis* was also inferred using the RCI. In this case, the RCI index is hereby referred to as "Tolerance," which represents a measure of the ability of the *P. australis* haplotype to tolerate resource competition with *S. alterniflora*.

Commented [JTC5]: Anthony, I've asked this before, but is the RCI based on above or belowground biomass. It seems like it should be based on both - have a RCI_B and RCI_A

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I conducted this experiment in a greenhouse setting in order to minimize variation in abiotic conditions (e.g. edaphic condition, water availability, nutrient availability) and biotic conditions (e.g. herbivory, presence of other plant species). By controlling for these sources of variation, any differences in the growth of *S. alterniflora* in the presence/absence of native or invasive haplotypes of *P. australis* can be attributed to the effects of competition~~, and vice versa~~.

Source of *P. australis*

Starting in the summer of 2009, a common garden was established at the South Campus of Louisiana State University that contained *P. australis* from a variety of locations and haplotypes. Haplotype for each source population was determined using the methods in Saltonstall (2002). Collected rhizome fragments were planted in 19 L pots containing Metromix 510 (Sun Gro Horticulture; Vancouver, Canada) in order to standardize soil conditions. The pots

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were then placed in shallow plastic pools (1.2 m in diameter, .25 m high) that were maintained with standing water. Over the ensuing 4 years, pots were split and replanted on occasion to minimize maternal effects and further increase the number of plants in the garden.

Spartina alterniflora as a phytometer

To bioassay competitive ability, we used *S. alterniflora*, a common wetland grass species known to occur in sympatry with both native and invasive haplotypes of *P. australis*. In this experiment, I used standardized 5 cm dormant plant plugs that were obtained from a commercial nursery (American Native Plants; Perry Hall, Maryland, USA), which sourced seed material from the northeastern coast of Virginia. All plant plugs were acclimatized in an incubator for a period of 7 days before being moved to the greenhouse for initiation of this experiment. ~~As this experiment was not designed to test the competitive interaction of *P. australis* and *S. alterniflora* across their ranges,~~ I specifically selected ~~a~~ the source of *S. alterniflora* to originate from the middle range of *P. australis* ~~in order to provide for a more controlled test~~. I note here that the relative strength of competition of *P. australis* in response to this species may change with if the source population of *S. alterniflora* changes.

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Experimental Set-up

For the greenhouse experiment, I used rhizome material from 14 *P. australis* populations that were growing in the common garden (Table 2). In December 2012, 9-11 g rhizome fragments from each population were grown in 55 cm X 45 cm X 18 cm polyethylene bus tubs filled with Metromix 510. Two months later (March, 2013), individual *P. australis* plantlets of native and invasive populations were re-potted in 1.9 L pots (with Metromix 510), either alone (no competitor = NC) or with *S. alterniflora* (SA). ~~The design was fully crossed such that each~~ *P. australis* haplotype (Native, Invasive, Gulf Coast, and None) was fully crossed with *Spartina* incidence (presence/absence). The exception was ~~Note: although~~ the *P. australis*-None and *Spartina*-absence combination, which was omitted. All treatment combinations were replicated 12 times per population.

Table 2. Source populations of *P. australis* used in the greenhouse experiment. Haplotype, nearest city to source population, latitude, and longitude are reported.

Commented [JTC7]: Which Native did you discard as contaminated? You should just delete that one from the paper entirely.

Designation	Haplotype Group	Location	Latitude	Longitude
APN	Native (F)	Appoquinimink, DE	39.44	-75.65
APM	Invasive (M)	Appoquinimink, DE	39.45	-75.64
PCI	Gulf Coast (I)	Pointe-Aux-Chenes, LA	29.45	-90.46
RCN	Native (F or AB)	Wells, ME	43.36	-70.48
PLM	Invasive (M)	Pass-A-Loutre, LA	29.13	-89.23
BSCM	Invasive (M)	Bath, ME	44.51	-70.35
SCM	Invasive (M)	Georgetown, SC	33.35	-79.26
NBM	Invasive (M)	New Brunswick, ME	46.10	-64.80
NBS	Native (S)	New Brunswick, ME	46.10	-64.80
NYM	Invasive (M)	Montezuma, NY	43.00	-76.70
FPM	Invasive (M)	Falmouth, MA	41.55	-70.60
FPN	Native (F)	Falmouth, MA	41.55	-70.60
RBI	Gulf Coast (I)	Cameron Parish, LA	30.18	-93.26
RRM	Invasive (M)	Cameron Parish, LA	29.68	-92.81

~~treatment combination was omitted, the treatment combination of *P. australis* None and *Spartina* presence was included as a control. All treatment combinations were replicated 12 times per population.~~

In order to ensure that nutrients were limiting, plants were grown in a nutrient-poor environment. Metro-mix 510 contains a limited amount of nutrients that should become depleted during the course of this experiment (L.A. Meyerson ~~personal communication~~unpubl. data) and no additional nutrients were added to the soil ~~medium~~ during the study. Because *P. australis* and *S. alterniflora* are semi-aquatic, pots were maintained in a wet environment by placing them into 1.5 L plastic containers filled with water. The position of the 348 pots within the greenhouse was determined using a random-number generator in order to minimize greenhouse effects. As needed, pots were sprayed with 51% Malathion to control for herbivorous insects (Ortho Max; The Scotts Company; Marysville, OH). Pots were randomly redistributed midway through the experiment to further minimize greenhouse effects. The experiment ran from March to July 2013, a duration of time sufficient for the plants to achieve maximum heights for the season (no significant difference in height between measurement periods).

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Data Collection

Initial measurements for stem height and number of stems for *P. australis* were taken during the first week after the start date of the experiment. Four weeks after the start of the experiment, potted *P. australis* and *S. alterniflora* were surveyed and the number of non-sprouting individuals was recorded. I measured stem height (to the nearest mm), number of stems, number of emerging stems, and number of dead stems for each plant species per pot. The same measurements were taken at bi-weekly intervals until the experiment was terminated. At the end of the experimental period, *S. alterniflora* and *P. australis* were harvested to obtain measurements of both aboveground and belowground biomass. For aboveground biomass, green sprouted stems were identified as belonging to either *P.australis* or *S. alterniflora* and clipped at soil level, after which they were placed in separate paper bags. For belowground biomass, *S. alterniflora* and *P. australis* root materials were hand separated, washed with tap water, and then placed into paper bags. Tissues were dried, either in an oven at 60 C or air dried on a greenhouse bench ~~Because *S. alterniflora* was smaller and required less space to dry, aboveground tissues were dried in an incubator at 60° C for a period of 7 days, whereas *P. australis* aboveground tissue was dried in the greenhouse for a period of 21 days. Belowground tissues for *S. alterniflora* were air dried in the greenhouse for a period of 14 days, whereas *P. australis* belowground tissue was dried in the same greenhouse for 25 days due to differences in overall belowground material~~. ~~All s~~Samples continued drying until ~~were reweighed until no~~no change in weight was detected in consecutive weighing periods.

The equation for the relative competition intensity index (RCI) for the effect of competition from either the native or invasive haplotype of *P. australis* on *S. alterniflora* was RCI = $(X_{NP}-X_{P})/X_{NP}$ where X is the biomass of *S. alterniflora* in the absence of *P. australis* (NP) and the presence of *P. australis* (P). RCI does not have a minimum value, but it does have a maximum value of 1 indicating the highest amount of competition (i.e., the competitor has zero biomass in the presence of *P. australis*). It ~~and~~ is a widely used metric for gauging competitive interactions between species (Goldberg et al. 1999). The RCI for the effect of *S. alterniflora* on *P. australis* (i.e., tolerance of competition with *S. alterniflora*) was also calculated ~~and interpreted in terms of the tolerance of *P. australis* to *S. alterniflora*~~using the same equation.

~~Because there was no flowering in the experimental pots due to the short duration of the~~

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Commented [JTC9]: Anthony, it may be best to report tolerance as 1-RCI. If you look at the figure for tolerance, then native has higher values. It's confusing. The native isn't more tolerant. What that graph is showing is the negative effects of spartina on Phragmites. By subtracting RCI from 1, then we get a measure that shows the invasive does better.

If you want to keep it as RCI, then don't call it tolerance, call it Spartina RCI (or RCI_S) as compared to RCI_P. This approach would be fine. If that's the case, you could state in this paragraph that from the perspective of Phragmites, 1-RCI_S would be a measure of their ability to tolerate resource competition with Spartina.

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~~experiment, aboveground and belowground biomass were selected as the best measures of fitness, and RCI was used to quantify competitive intensity.~~

Statistical Analyses

The experiment was designed such that the effects of *P. australis* haplotype (~~fixed factor~~native or invasive) and latitude (covariate) on plant ~~performance~~ biomass (above- or below-ground) or RCI would be assessed with a nested ANCOVA. In this case, source population was nested within haplotype. The reason for this nesting is that the 12 replicate pots per treatment combination (*P. australis* haplotype - *Spartina* incidence treatments) cannot be considered independent replicates because they derive from the same field collection of rhizome material (and are likely genetically identical). Consequently, the true unit of replication is the population. The nested ANCOVA properly deals with this nonindependence among replicates within a population. However, owing to the strongly unbalanced design, (Native haplotypes N = 3, ~~Gulf Coast haplotypes N = 2,~~ Invasive haplotypes N = 8) and relatively low number of native populations, it was not possible to conduct this analysis. Therefore, to avoid the possibility of pseudoreplication, I computed the mean response among the 12 replicates per source population and performed a simpler one-way ANCOVA with haplotype, latitude of origin, and the haplotype-by-latitude interaction term as the independent variables. *F*-statistics were computed using Type III sums of squares which are appropriate for unbalanced designs (Johnson and Bhattacharyya 2009). Finally, I determined the relationship between dependent variables (aboveground biomass, belowground biomass, RCI) ~~was regressed against latitude and the total biomass of *P. australis* to determine the correlation between each on competitive intensity~~using Pearson's product-moment correlations.

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I used Akaike's Information Criterion, AIC (Akaike 1973) to select the best model to explain the variation in *P. australis* aboveground and belowground biomass, RCI and tolerance, based on all possible combinations of the independent variables. ~~For both the *S. alterniflora* dataset and the *P. australis* dataset, the constructed ANOVA models using all independent variables and their possible combinations were evaluated for usefulness in explaining observed patterns. Because fewer than 4 explanatory variables were considered, I was able to run all possible model combinations and evaluate them using Akaike Information Criterion (Burnham and Anderson 2002). After all models were constructed, the Akaike's Information Criterion, AIC (Akaike 1973), for each model was obtained from the output and compared using the~~ AIC$_c$ for small sample size was used (Burnham and Anderson 2002). The best model was selected based on corrected ~~-~~Akaike weights~~ as well as evidence ratios were calculated in order to assist with model selection.~~

~~All values for both aboveground and belowground biomass were transformed using the natural log to attain a normal distribution. All analyses were conducted using the General Linear Models procedure in Systat 12 (Systat Software, San Jose, CA).~~

The Gulf Coast haplotype was withheld from the previous ~~latitudinal~~ analyses because the populations originated from a very small latitudinal range in southern Louisiana. ~~-~~In order to compare competitive ability among the ~~examine differences in competitive ability and biomass production between all~~ three haplotypes (native, invasive, Gulf Coast), I did the following. I performed separate regression analyses for the effects of latitude on biomass (above- and below-ground), RCI or tolerance. The residuals from these regressions, which have factored out the effects of latitude on the dependent variables, were then used in separate one-way ~~sets of~~

ANOVA models with haplotype as the independent effect. ~~based on the residuals from a regression analysis were~~ used. ~~The Gulf Coast haplotype was withheld from the previous latitudinal analyses because the populations originated from a very small latitudinal range in southern Louisiana. For comparisons of the Gulf Coast haplotype with the other haplotypes, I first removed the effects of latitude by obtaining the residuals from regressions of latitude against RCI, aboveground biomass, and belowground biomass for each haplotype. Next, I used the residuals to construct ANOVA models that compared differences in RCI, and *S. alterniflora* fitness between all three haplotype groups.~~

All values for both aboveground and belowground biomass were transformed using the natural log to attain a normal distribution. All analyses were conducted using the General Linear Models procedure in Systat 12 (Systat Software, San Jose, CA).

~~For both the *S. alterniflora* dataset and the *P. australis* dataset, the constructed ANOVA models using all independent variables and their possible combinations were evaluated for usefulness in explaining observed patterns. Because fewer than 4 explanatory variables were considered, I was able to run all possible model combinations and evaluate them using Akaike Information Criterion (Burnham and Anderson 2002). After all models were constructed, the Akaike's Information Criterion, AIC (Akaike 1973), for each model was obtained from the output and compared using the~~ ~~AIC_c~~ ~~for small sample size (Burnham and Anderson 2002). Akaike weights as well as evidence ratios were calculated in order to assist with model selection.~~

~~All values for both aboveground and belowground biomass were transformed using the natural log to attain a normal distribution. All analyses were conducted using the General Linear Models procedure in Systat 12 (Systat Software, San Jose, CA).~~

RESULTS

Effects of Invasive and Native *P. australis* on *S. alterniflora*

P. australis had a significant negative effect on both the aboveground and belowground biomass of *S. alterniflora* (Table 3). Of the possible candidate models for predicting *S. alterniflora* aboveground biomass (supplemental Table 1), the best model (model 6) incorporated haplotype, latitude, and the interaction between haplotype and latitude ~~(Table 2)~~. This best model was 1.289 and 1.931 times more likely than the next most plausible models (models 2 and 4, respectively). ~~Overall, evidence supported the inclusion of haplotype across all three models and indicates that *S. alterniflora* biomass when grown with *P. australis* depends primarily on haplotype.~~ In the best model, ~~for *S. alterniflora* aboveground biomass~~ haplotype, latitude, and haplotype-by-latitude ~~all had a significant effect on the aboveground biomass of Spartina;~~were statistically significant and ~~explaining~~ explained 26%, 38%, and 34% of the variation in *S. alterniflora* aboveground biomass, respectively (Table 3). Overall, the three best models supported the inclusion of *P. australis* haplotype suggesting that *S. alterniflora* biomass depends primarily on *P. australis* haplotype with which it is grown. There was a 92% reduction in *S.*

Commented [JTC10]: aren't you supposed to provide a table of all possible models, probably as an appendix?

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Commented [JTC11]: where is the evidence to support this?

Commented [JTC12]: where is the evidence to support this?

Commented [JTC13]: More variation is explained by latitude or the interaction. Why do you conclude that haplotype is the most important variable?

alterniflora aboveground biomass production when it was grown with the invasive haplotype as opposed to the native haplotypes (Fig. 2). Whether it ~~is~~ was grown with the native or invasive haplotype of *P. australis*, the aboveground biomass of *S. alterniflora* increased with increasing latitude of origin. Interestingly, the effects of latitude on aboveground biomass were more pronounced for the native than the invasive haplotype, such that the latitudinal cline in aboveground biomass was steeper for the native haplotype; hence the significant haplotype-by-latitude interaction (Fig. 2).

For *S. alterniflora* belowground biomass, the top model (model 5) included only haplotype and latitude (Table 2). ~~The top model was 1.026 and 3.67 times more likely than the~~~~Contrary to what was found with aboveground biomass, haplotype of *P. australis* was a bigger factor affecting belowground biomass of *S. alterniflora* than latitude (69% vs. 28%) (Table 3).~~ The top model was 1.03 and 3.67 times more likely than the next two most plausible models (models 4 and 2), which incorporated the haplotype by latitude interaction term and haplotype, respectively. As before, haplotype was supported across all plausible models. In comparison, latitude was a component of the top two models but was not a statistically significant factor in the best-fit model (Table 3). Haplotype of *P. australis* was explained more than twice the variation in S. alterniflora belowground biomass than latitude (69% vs. 28%) (Table 3). ~~Again, haplotype is supported across all plausible models, however, latitude was also a component of the most similar top two models but was not a significant effect and thus the production of *S. alterniflora* belowground biomass when grown with *P. australis* depends on the haplotype of *P. australis*.~~ W~~Consequently, w~~hen *S. alterniflora* ~~is~~was planted with the invasive haplotype it produces 52% less biomass than when planted with the native haplotype (Fig. 3).

~~The top model (model 5) for *S. alterniflora* belowground biomass included only haplotype and latitude (Table 2).~~ ~~The top model was 1.026 and 3.67 times more likely than the~~

Table 3. Results from the AIC_c model selection for *S. alterniflora* aboveground biomass, belowground biomass, RCI, *P. australis* aboveground biomass, belowground biomass, and tolerance. ~~Explanation of column headings:~~ K is the number of parameters, AIC_c is the corrected Akaike's Information Criterion, $\Delta i AIC_c$ is the difference between the lowest AIC_c score and the AIC_c score of each model (model *i*), Akaike's weight (w_i) is the weight in favor of model *i*, the evidence ratio is the number of times more likely the top-selected model is relative to model *i*. Top models are highlighted in bold.

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Model no.*	K	Variables	AIC_c	$\Delta_i AIC_c$	w_i	Evidence Ratio	Adj. R^2	Model Rank
S. alterniflora Aboveground Biomass								
6	**4**	**Haplotype, Latitude, Haplotype*Latitude**	**2.216**	**0.000**	**0.420**	**1.000**	**0.97**	**1**
2	**2**	**Haplotype**	**2.724**	**0.508**	**0.326**	**1.289**	**0.90**	**2**
4	**2**	**Haplotype*Latitude**	**3.532**	**1.316**	**0.218**	**1.931**	**0.88**	**3**
S. alterniflora Belowground Biomass								
5	**3**	**Haplotype, Latitude**	**-0.114**	**0.000**	**0.410**	**1.000**	**0.86**	**1**
4	**2**	**Haplotype*Latitude**	**-0.063**	**0.051**	**0.400**	**1.026**	**0.76**	**2**
2	**2**	**Haplotype**	**2.488**	**2.602**	**0.112**	**3.673**	**0.68**	**3**
RCI								
6	**4**	**Haplotype, Latitude, Haplotype*Latitude**	**-16.994**	**0.000**	**0.923**	**1.000**	**0.98**	**1**
4	2	Haplotype*Latitude	-10.745	6.249	0.041	22.749		2
2	2	Haplotype	-10.392	6.602	0.034	27.140		3
P. australis Aboveground Biomass								
5	**3**	**Haplotype, Latitude**	**-10.390**	**0.000**	**0.575**	**1.000**	**0.95**	**1**
8	**4**	**Haplotype, Latitude, Spartina**	**-9.151**	**1.239**	**0.310**	**1.858**	**0.95**	**2**
10	**4**	**Haplotype, Latitude, Haplotype*Latitude**	**-8.566**	**1.824**	**0.231**	**2.489**	**0.95**	**3**
P. australis Belowground Biomass								
6	**3**	**Haplotype, Spartina**	**-13.260**	**0.000**	**0.419**	**1.000**	**0.95**	**1**
2	**2**	**Haplotype**	**-12.873**	**0.387**	**0.345**	**1.213**	**0.95**	**2**

(Table 3 continued)

8	4	Haplotype, Latitude, Spartina	-10.007	3.253	0.082	5.086		3
Tolerance								
5	**3**	**Haplotype, Latitude**	**-27.854**	**0.000**	**0.775**	**1.000**	**0.95**	**1**
6	4	Haplotype, Latitude, Haplotype*Latitude	-24.810	3.044	0.169	4.581		2
2	2	Haplotype	-22.584	5.270	0.056	13.943		3

* See Supplemental Table 1 for a description of the suite of models used in these analyses.

Table 4. Top-ranked GLM models for both mean *S. alterniflora* aboveground and belowground biomass (Models X & X, respectively). *P*-values that are significant following a Bonferroni correction are highlighted in bold. % -Effect size is the percentage variation explained and based on the mean squares error for each source divided by the total mean squares.

Source	DF	Means Squares	F	P-value	% ~~Effect Size~~Var Explained
S. alterniflora Aboveground Biomass					
Haplotype	1	0.168	11.017	**0.013**	26.08
Latitude	1	0.243	15.975	**0.005**	37.73
Haplotype*Latitude	1	0.218	14.288	**0.007**	33.85
Error	7	0.015	-	-	2.33
S. alterniflora Belowground Biomass					
Haplotype	1	0.437	20.819	**0.002**	69.04
Latitude	1	0.175	8.317	0.020	27.65
Error	8	0.021	-	-	3.32

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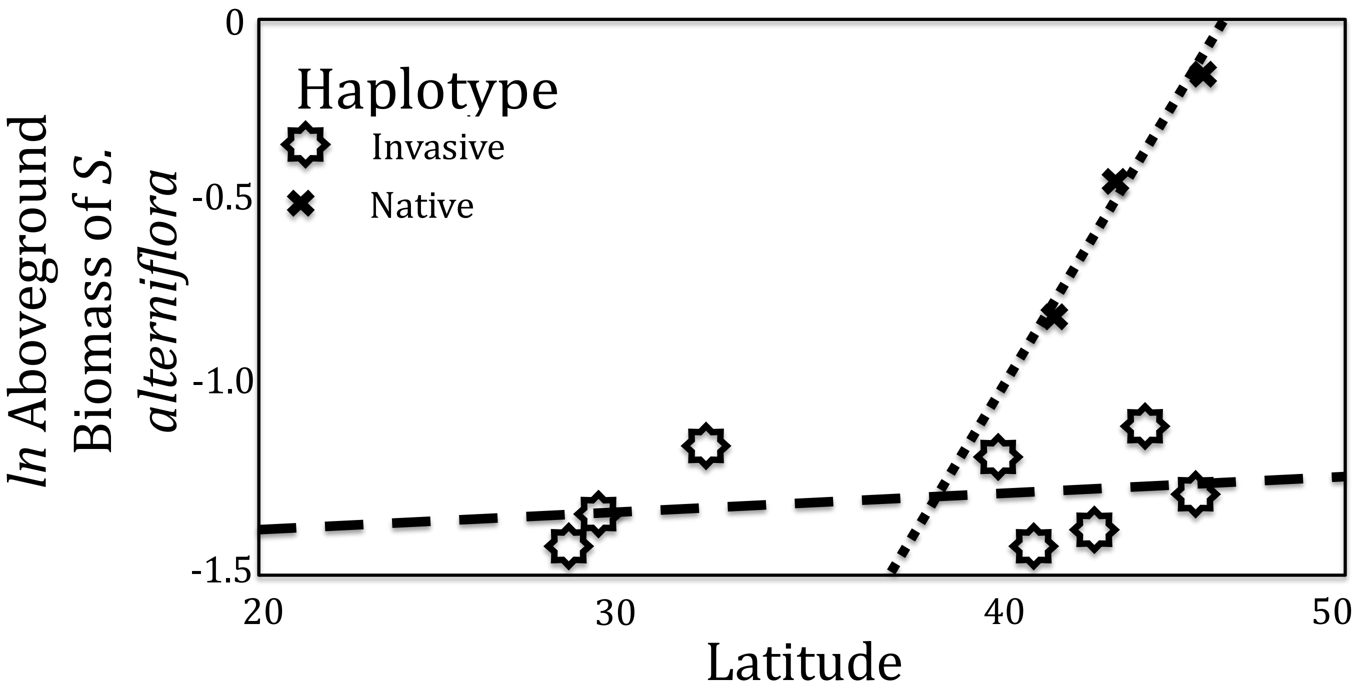

Figure 2. ~~Linear r~~Relationship between latitude and aboveground biomass production by *S. alterniflora* (ln-transformed) when grown with either the invasive or native haplotype of *P.australis*. Values are based on the least squares means and ~~.~~lines are fit by least-squares regression.

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~~next two most plausible models (models 4 and 2), which incorporated the haplotype by latitude interaction term and haplotype, respectively. Again, haplotype is supported across all plausible models, however, latitude was also a component of the most similar top two models but was not a significant effect and thus the production of *S. alterniflora* belowground biomass when grown with *P. australis* depends on the haplotype of *P. australis*. Consequently, when *S. alterniflora* is planted with the invasive haplotype it produces 52% less biomass than when planted with the native haplotype (Fig. 3).~~

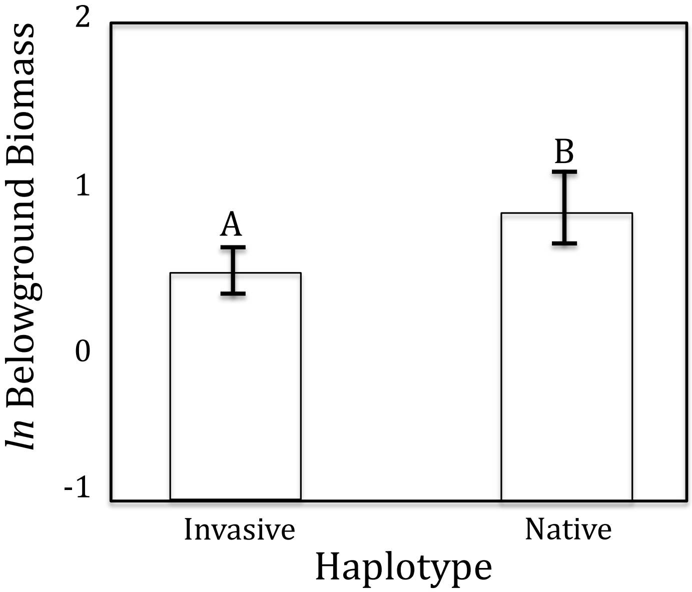

Figure 3. ~~Least-squares means of b~~Belowground biomass of *S. alterniflora* (ln-transformed least-squares means) when grown with either the invasive or native haplotype of *P. australis*. Different letters indicate a significant difference. Error bars represent 95% CI.

Of paramount importance in influencing t~~T~~he RCI of *P. australis* (i.e., the negative effects of *P. australis* on *S. alterniflora*) was ~~similar to aboveground and belowground biomass~~

~~in how it was affected primarily by~~ haplotype ~~and to a lesser degree~~followed by latitude. ~~In regards to the RCI, m~~Model 6 was ~~the~~ deemed the only ~~top~~ viable model based on AIC$_c$ weights and included haplotype, latitude, and the haplotype-latitude interaction ~~term~~. The RCI of the invasive haplotype was 19% greater than the RCI ~~from~~ of native haplotypes. Notably, there was no evidence that the RCI changed with latitude in the invasive haplotype, however, there was a sharply declining trend in the RCI of the native haplotypes with increasing latitude (Fig. 4). Consequently, the haplotype by latitude interaction term explained the greatest amount of variation (36%) in RCI (Table X).

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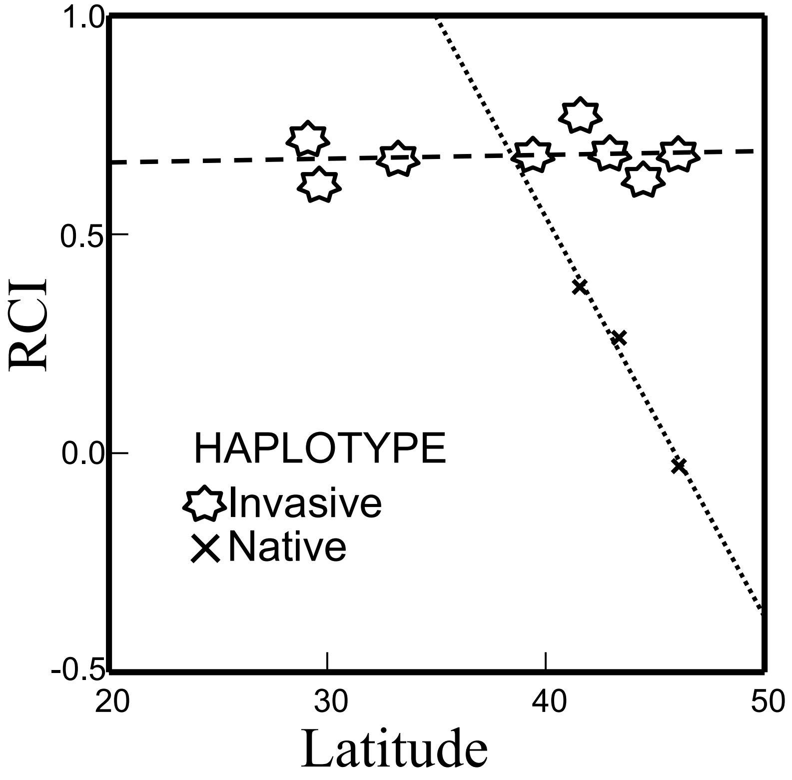

Figure 4. The ~~linear~~ relationship between relative competitive intensity (RCI) of native and invasive *P. australis* and latitude. Values are based on the least squares means and lines are fit by least-squares regression.

P. australis biomass production in the presence of *S. alterniflora*

Aboveground biomass production of *P. australis*, in the presence of ~~The differences in the competitive impact of *P. australis* on~~ *S. alterniflora*, was ~~corresponded to the differences in biomass between the two haplotypes of *P. australis*. The top~~ influenced by ~~model (model 5) for *P. australis* aboveground biomass included only~~ haplotype and latitude (model 5; Table 5). The next two most plausible models (models 8 and 10) each included either ~~*Spartina*~~ *S. alterniflora* or the interaction term between haplotype and latitude. However, each of these effects when included in the model were non-significant. Therefore, the top three models together provided strong support for the effect of haplotype as a primary ~~effect and latitude as a covariate effect on the production of~~factor affecting *P. australis* aboveground biomass. ~~*S. alterniflora* did not significantly affect the production of *P. australis* biomass.~~ The invasive haplotype achieved 45% greater aboveground biomass than the native haplotype (Fig 5). Aboveground *P. australis* biomass decreased with increasing l~~In addition to haplotype, l~~atitude ~~was the only other variable to affect the aboveground biomass of *P. australis* and~~but this variable explained only 14% of the variation in biomass production (Table 5).

Similarly, h~~The h~~aplotype of *P. australis* was also the most important factor affecting the production of *P. australis* belowground biomass. The top model (model 6) ~~for belowground biomass~~ included haplotype and ~~*Spartina*~~*S. alterniflora*, and was 1.21~~3~~ times more likely than the only other plausible model (model 2) that only included haplotype. ~~Although,~~In the top

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model, ~~included~~ the presence of *S. alterniflora* ~~as an effect it~~ was not significant (Table 5). ~~Therefore, the differences in *P. australis* belowground biomass were best explained by haplotype. A~~A 50% difference in belowground biomass was present between the larger and more competitively superior invasive haplotype and the smaller native haplotypes (Fig. 6). ~~Furthermore~~Finally, RCI was highly correlated with the total amount of *P. australis* biomass (R^2 = 0.797, P-value = < .001) ~~as opposed to latitude (R^2 = 0.165, P = 0.215)~~.

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Table 5. Top-ranked GLM models for mean *P. australis* aboveground (Model 5) and belowground biomass (Model 6). Models include the effects of haplotype and latitude on aboveground biomass; and haplotype and the presence of *S. alterniflora* for belowground biomass. *P*-values that are significant following a Bonferroni correction are highlighted in bold. Effect size is the percent variation explained and based on the mean squares error for each source divided by the total mean squares.

Source	DF	Mean Squares	*F*	*P*-value	Effect Size
Aboveground Biomass					
Haplotype	1	2.366	89.603	**< 0.001**	85.32
Latitude	1	0.381	14.423	**0.001**	13.74
Error	19	0.026	-	-	0.94
Belowground Biomass					
Haplotype	1	4.589	198.008	**< 0.001**	97.93
~~*Spartina*~~*S. alterniflora*	1	0.074	3.181	0.090	1.58
Error	19	0.023	-	-	0.49

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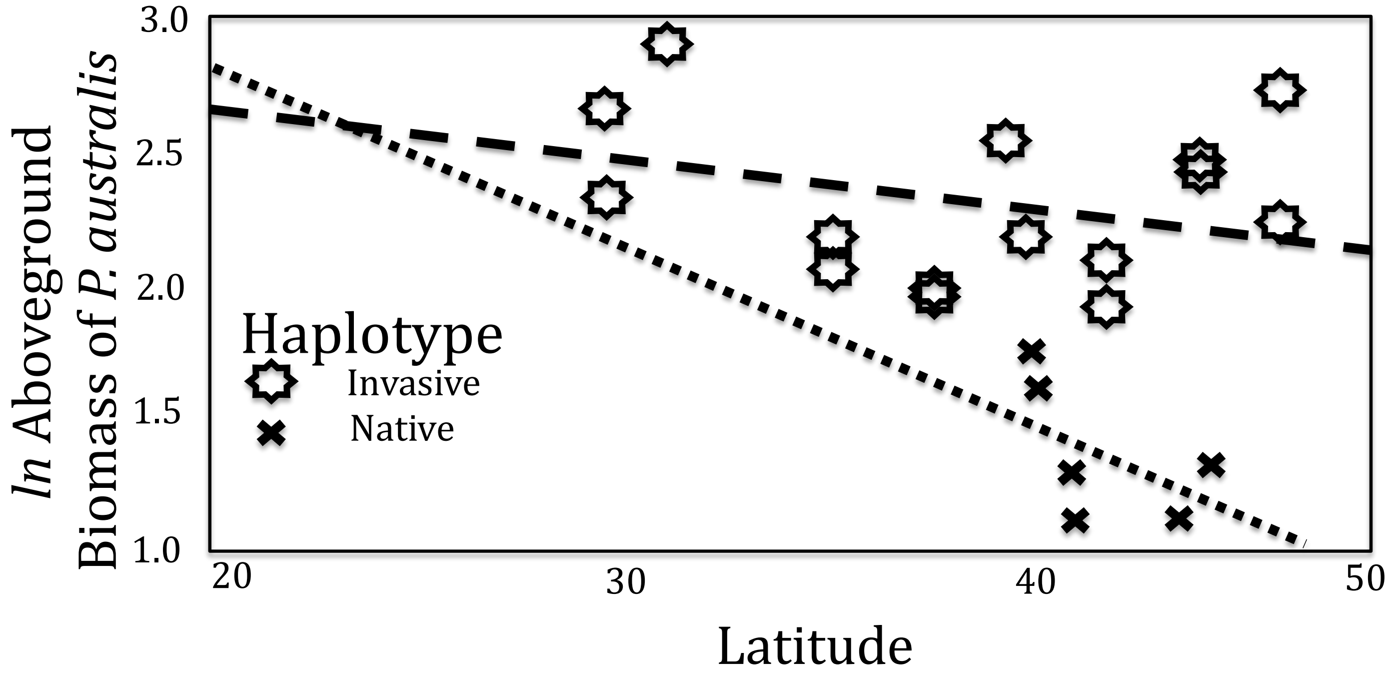

Figure 5. Linear relationship between latitude and aboveground biomass production by *P. australis* when grown in the presence of *S. alterniflora*. Values are based on the least squares means.

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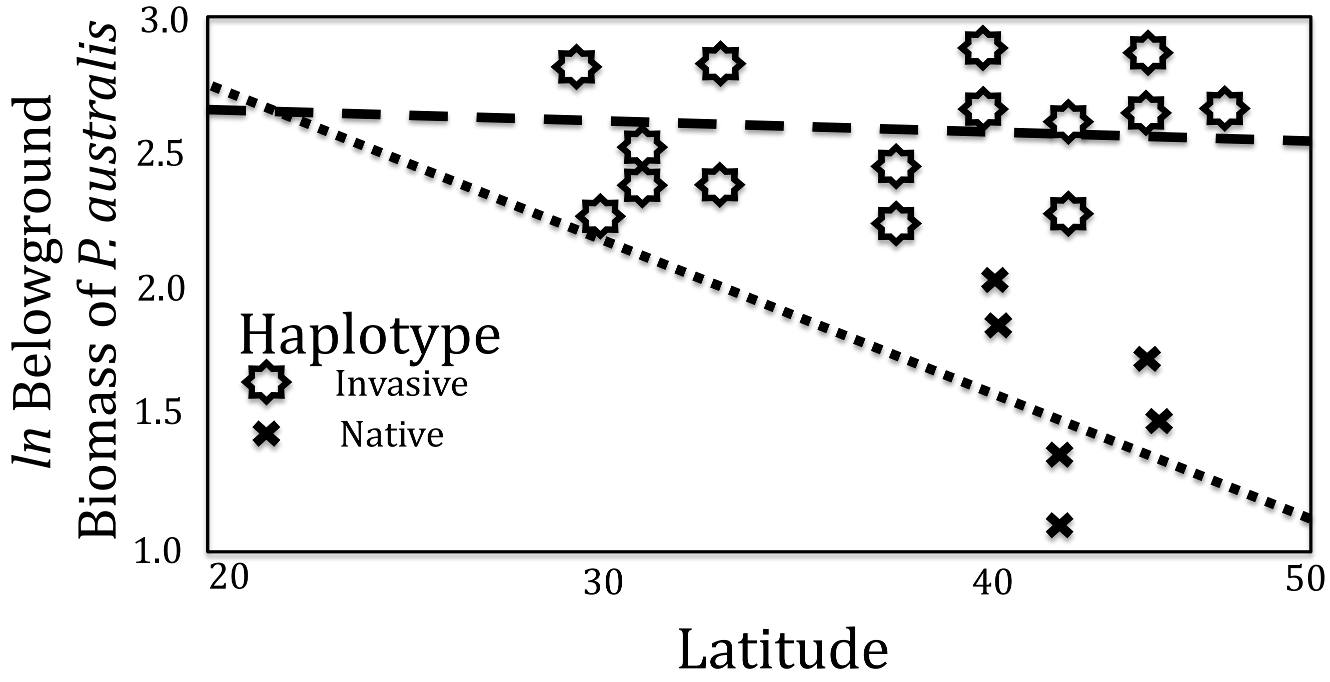

Figure 6. Linear relationship between latitude and belowground biomass production by *P. australis* when grown in the presence of *S. alterniflora*. Values are based on the least squares means.

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Overall, *P. australis* was little affected by the presence of ~~The effect of *S. alterniflora* on *P. australis* was minimal, however, there were differences in the response of each haplotype to *S. alterniflora*. The presence of *S. alterniflora* and its effect was either not a component of a top model (e.g., aboveground biomass) or was not significant when included in the model (e.g., belowground biomass).~~ *S. alterniflora*. Although there was no significant effect of *S. alterniflora* on the overall growth of *P. australis*, the effect of *S. alterniflora* was 58% higher in the native haplotype of *P. australis* than the invasive haplotype and in both haplotypes decreased with latitude (Figure 7). Regardless of haplotype, the effect of *S. alterniflora* on overall *P. australis* biomass production increased with latitude (Figure 7).

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Commented [JTC20]: something is missing here. I assume that you are talking about tolerance, but it is never mentioned. Also, shouldn't you have done an AIC analysis of different models? What about an ANOVA table?

The Competitive Effect of the Gulf-Coast Haplotype

In a comparison among the three main *P. australis* haplotypes, native, invasive and Gulf Coast, the~~The~~ Gulf Coast haplotype ~~of *P. australis*~~ was intermediate in its effects on *S. alterniflora* above- and below-ground biomass (Figure 9) and had intermediate competitive ability (RCI; Figure 8). In none of the cases was the Gulf Coast haplotype significantly different from the native or invasive haplotype. ~~not significantly different from the native or invasive haplotypes in terms of competitive ability. Although not significantly different, the RCI of the Gulf Coast haplotype was intermediate between the native and invasive haplotypes (Figure 8). Correspondingly, the growth of *S. alterniflora* in the presence of the Gulf Coast haplotype was greater than when in the presence of the invasive haplotype, but less than when in the presence of the native haplotype (Figure 9).~~

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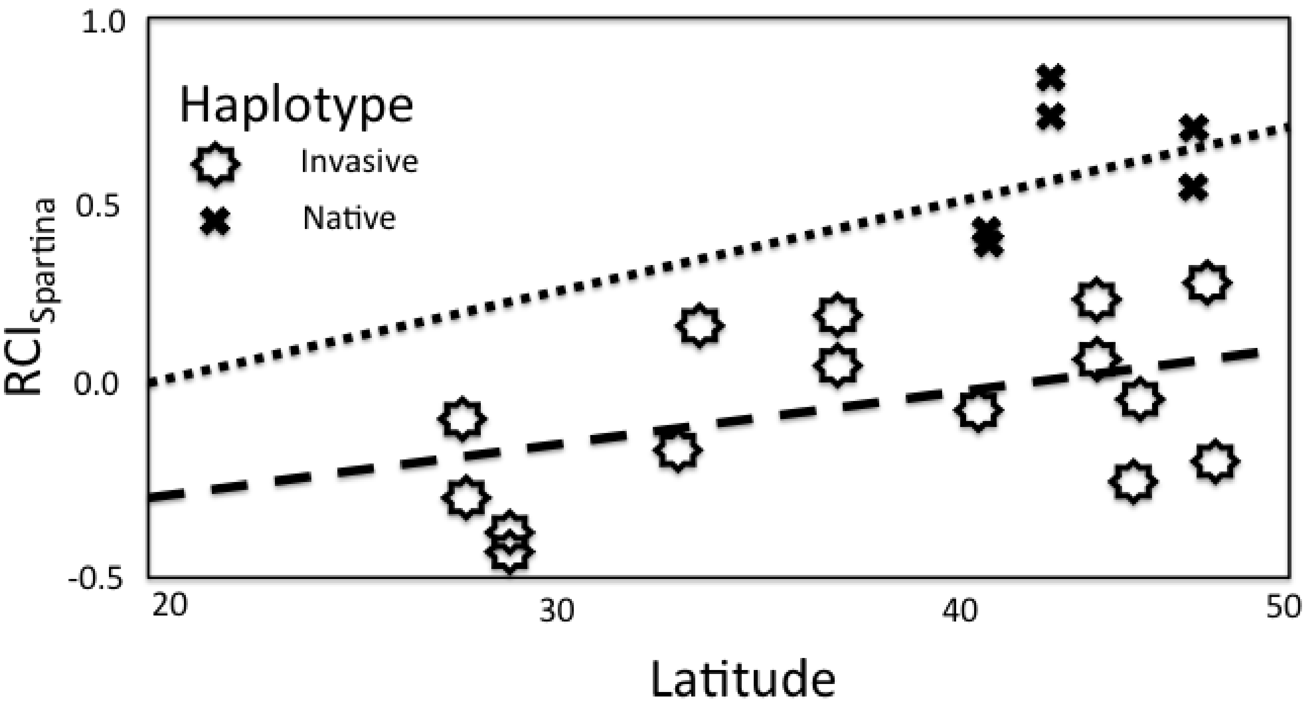

Figure 7. Linear relationship between the relative competitive intensity of *S. alterniflora* on *P. australis* and latitude. Values are based on the least-squares means.

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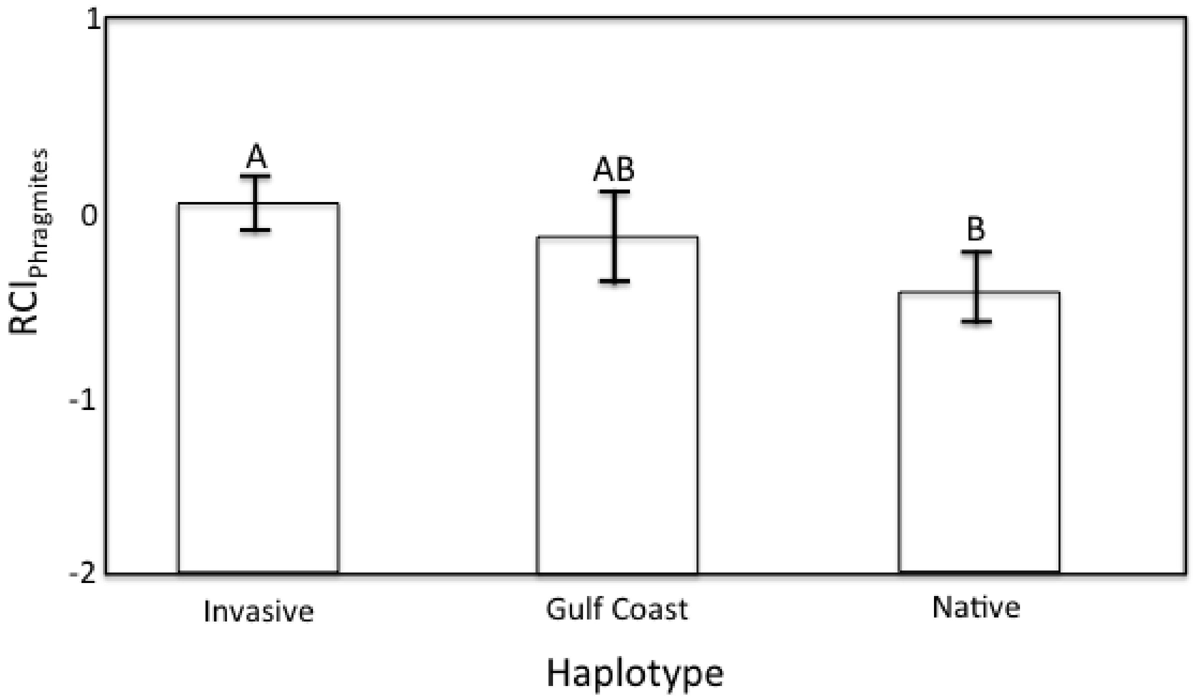

Figure 8. Least-squares means of the relative competitive intensity of the three major haplotype groups of *P. australis*. Different letters indicate a significant difference. Error bars represent 95% CI.

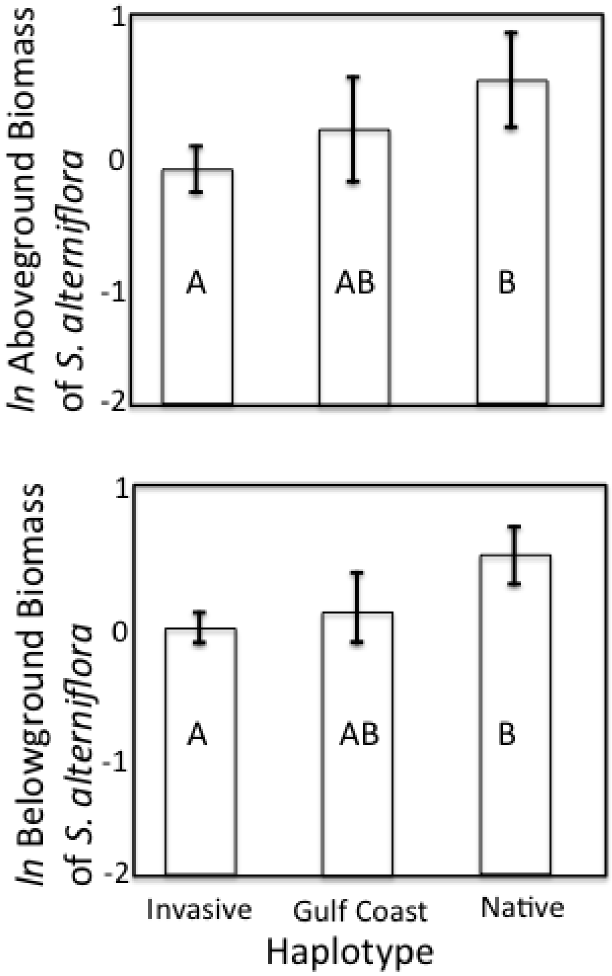

Figure 9. Least-squares means of both aboveground and belowground biomass of *S. alterniflora* in the presence of the three major haplotypes groups of *P. australis*. -Different letters indicate a significant difference. Error bars represent 95% CI.

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DISCUSSION

This is the first study to demonstrate that the relative competitive ability of native and invasive taxa varies with latitude, which can have important implications for invasion success (see Fig. 1). Although the competitive ability of both native and invasive haplotypes changed with latitude, as illustrated by Fig. 1, changes were not in parallel. Unlike the competitive ability of other species (Table 1) and the native haplotype of *P. australis*, the competitive ability of the invasive haplotype does not exhibit a latitudinal cline in competitive ability. ~~Therefore, as highlighted in Fig. 1,~~A ~~a~~t more northerly latitudes, invasion success may have been fostered by a strong competitive advantage to the invasive haplotype. In contrast, at lower latitudes, the native and invasive haplotypes are more similar in competitive ability and invasion success may not have been achieved as a result of competitive superiority to native *P. australis.*

Commented [JTC25]: Anthony, what happened with this Discussion? 2 1/2 pages for the first paragraph - really? It needs way more work than I can do just by shuffling around some text.

Commented [JTC26]: I was unaware that any of your data showed that the invasives exhibited latitudinal variation in competitive ability.

Because competitive ability is strongly correlated with plant size, this study also supports the hypothesis that the size advantage of the invasive over the native haplotypes may be the determining factor behind the former's superior competitive ability (Dostal 2011). Overall, this study highlights the importance of a large-scale, biogeographic approach to studying biological invaders. Due to the large geographic ranges over which invasive species can be found, variation in factors such as biotic resistance can impact the probability of invasion success over broad latitudinal scales (Sax 2001). Furthermore, the observation that invasive species are more prevalent at temperate rather tropical latitudes (Sax 2001) fits with the observation that the latitudinal range of non-native plants in their introduced range extends polewards instead of towards the Equator (Guo et al. 2012). Although native species evolve over time in response to latitudinal differences in biotic and abiotic factors, invasive species are unable to evolve to the same type of influences by virtue of being introduced and relatively novel to a range. As

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Commented [JTC27]: I think that this idea needs more clarity. Guo found that invasives generally exhibited northward shifts. That fits perfect with Phragmites and your results about competition.

Your text is confusing the situation. Our whole research area is in the temperate zone and we have no tropical comparison. So, based on your arguments, it's hard to interpret the phragmites data. Reread the Guo paper.

Commented [JTC28]: See my comments in Discussion outline about evidence for rapid evolution in invasives.

opposed to the native haplotype, the invasive haplotype of *P. australis* has only been detected in North America since the early 19th century (Saltonstall 2002). Therefore, the native populations of *P. australis* have had a significantly longer amount of time to evolve in response to the abiotic and biotic conditions in North America than the invasive haplotype. Upon arrival, invasive species may be better competitors than resident natives, however, at certain points along a latitudinal gradient there may exist areas of higher biotic resistance (lower latitudes) and areas of lower biotic resistance (higher latitudes) based on the cumulative competitive ability of all native species in a given location. Similar to the findings in Fine (2002) and Freestone et al. (2013) that demonstrate higher biotic resistance at lower latitudes, the findings in this experiment support the possibility of higher biotic resistance at lower latitudes as a result of stronger competition from native species at such latitudes. Based on our model predictions (Fig x), we might expect that ~~Based off the trend of increasing competitive ability with decreasing latitude,~~ native populations of *P. australis* from latitudes lower than those used in this experiment ~~should either~~might display ~~equal or~~ greater competitive ability against *S. alterniflora* than the invasive haplotype. ~~For example, the native haplotypes of *P. australis* could possibly outcompete the invasive haplotype of *P. australis* against *S. alterniflora* below the 40th parallel (e.g., native populations of *P. australis* found in North Carolina at a latitude of 35.5°). These findings may help to explain why the invasive haplotype of *P. australis* is found only as far south as the southernmost portions of Louisiana but not in the subtropical regions of Florida. Furthermore, based off the introduction time (early 19th century) and location (northeast Atlantic coast), the invasive haplotype has had only slightly longer period of time in which to evolve in response to northern populations of native species than southern populations.~~ Similarly, other species that are introduced at higher latitudes from northern source populations would require more time to adapt

Commented [JTC29]: I've said this before. You need to be really careful about discussions of biotic resistance. You have no evidence. You have strong evidence that the exotic is a better competitor and that its competitive advantage wanes as latitude decreases. But, not a single iota of data in support of biotic resistance. Absolutely nothing! I've said this in every previous draft as well. You are extrapolating beyond your data!!

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to the competitive ability in southern native populations, and vice versa depending on introduction location and the location of origin.

The significant correlation between size and competitive ability demonstrated in this study corresponds well to the findings of Vila and Warner (2004) and Dostal (2011) in that the invasive haplotype of *P. australis* produced significantly ~~greater amounts of~~more biomass and was a significantly better competitor. ~~Although other studies have shown that increased competitive ability results from faster growth in invasive species relative to slower growth in natives (Graebner et al. 2012), the results from this study further support the link between competitive ability and growth through the use of native, introduced, and invasive haplotypes of the same species. Whereas the smaller slower growing native haplotypes had the lowest competitive ability as expected, the faster growing invasive haplotypes possessed the greatest competitive ability. In essence, it is possible that the invasive and introduced haplotypes are better competitors than native haplotypes across a range of abiotic conditions (e.g., nutrient availability) due to their size.~~ In nutrient poor conditions where the importance of competition likely shifts to belowground resources, the higher belowground biomass of the invasive haplotype may confer a competitive advantage. Conversely, in nutrient rich conditions, the significantly greater amount of aboveground biomass produced by the invasive haplotype may confer a competitive advantage for light acquisition (Goldberg 1996). Overall, my finding that the invasive haplotype has greater competitive ability than native haplotypes of *P. australis* is consistent with other studies involving *P. australis* (Bakker and Wilson 2001; Gorchov and Trisel 2003; Blank 2010; French 2012; Leicht-Young et al. 2012). In the presence of the invasive and introduced haplotypes of *P. australis, S. alterniflora* produced less biomass than when in the presence of the native haplotype; thus indicating the potential for significant

Commented [JTC30]: I really don't like this. There's a great deal of circularity in your argument. RCI is based on plant size and RCI is correlated with plant size. Is that surprising? Don't go overboard with this Discussion topic.

negative impacts on *S. alterniflora* in natural systems and the promotion of invasion success due to the slow competitive exclusion of native species (Burdick and Konisky 2003; Loehle 2003).

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Commented [JTC32]: OK, here you are talking about haplotype differences in competition. This should come before your discussion about the relationship between biomass and competitive ability. See Discussion outline.

There is a growing list of haplotypes of *P. australis* being reported in North America, but most attention has been paid to native-invasive comparisons. The Gulf Coast haplotype is widespread and common but has received little attention in studies of competitive ability. Although studies exist demonstrating the growth differences of the Gulf Coast haplotype relative to other wetland plant species and the invasive haplotype of *P. australis* (Howard and Rafferty 2006; Howard et al. 2008; Howard 2010), a comparison of competitive ability ~~between the two~~ among all three haplotypes was lacking. Although the RCI of the Gulf Coast haplotype is not significantly different from either the native haplotype or the invasive haplotype, it does appear to be intermediate between the native and invasive haplotypes. The intermediate position of the Gulf Coast haplotype on a parsimony network of identified *P. australis* haplotypes corresponds to its intermediate growth and competitive ability (Saltonstall 2002).

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~~The success of a biological invasion is contingent on a variety of factors, and the results from this study indicate that the physiological and geographical properties of an invasive species must be taken into consideration.~~ An important consideration that must be pointed out is that my conclusions are likely to change with the species and origin of the test plant used to assess *P. australis* competitive ability (i.e., *S. alterniflora*). Many possible species that are widely co-distributed with *P. australis* could have been used; e.g., *Typha* sp. ~~Although the results from this experiment may apply only to~~ *S. alterniflora*~~, which~~ has been shown to be an ~~is normally an~~ inferior competitor to both native and invasive varieties of *P. australis* (Emery et al. 2001; Burdick and Konisky 2003). As suggested by Table 1, it is also likely that southern or northern population of *S. alterniflora* would differ in their ability to compete with *P. australis*. My study

Commented [JTC33]: What physiological work have you done in this paper?

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was a starting point to explore the potential differences in competitive ability of native and invasive haplotypes of *P. australis* over the invasion range of this species in North America. This study clearly demonstrates the potential for non-parallel mismatches in competitive ability of native and invasive species (or haplotypes) that may be critical to invasion success. More studies are clearly needed to explore how the site of origin and invasion might affect competitive interactions with a variety of species.~~, the overall finding concerning competitive ability and latitude between native and invasive plants are likely to be applicable to other species especially, if the goal is to minimize the spread of invasive species. For example, certain fast growing annuals such as *Lolium multiforum* (Italian Ryegrass) and *Bidens cernua* (Nodding Beggartick) provide biotic resistance against *P. australis* by having a higher growth rate thus pre-empting it for resources and negating its size advantage (Byun et al. 2013). Therefore, the establishment or transplant of native, fast growing annuals from southern latitudes to northern latitudes may serve as effective bulwarks against the further spread of invasive *P. australis*.~~

Commented [JTC34]: Still needs some fine tuning, but you get the point.

Commented [JTC35]: Way too speculative.

~~Finally, it should be noted that in this experiment, the primary focus was on the competitive ability between native and invasive congeners of the same species on a naturally co-existing competitor. Therefore, results from this experiment apply primarily to effects of these congeners on other species (e.g., interspecific competition). However, it should be noted that the inferences about the competitive ability of the haplotypes of *P. australis* are based on single standardized test species (*S. alterniflora*). To confirm the patterns found in this study, the author recommends examining whether the competitive ability of a broader group of invasive species in relation to other co-occurring native species also varies over latitude.~~

Commented [JTC36]: Merge with the previous paragraph.

~~In certain cases, similarity between resident natives and an invading species may provide the most resistance against invasion due to competition for the same resources (Bakker and~~

~~Wilson 2004; Dukes 2002). When *P. australis* attempts to establish or invade increasingly southern latitudes, there should be a high degree of intraspecific competition because the Gulf Coast haplotype is much more prevalent at lower latitudes than the native haplotype. Furthermore, the RCI and size of the Gulf Coast haplotype is not significantly different from the invasive haplotype. Therefore, an effort should be made to examine the effect of size differences and latitude on competitive ability within the invasive haplotype of *P. australis*, and then gauge how these variations may influence establishment of invasive *P. australis* into southern populations comprised of either the Gulf Coast or native haplotypes.~~

Conclusions

Overall, ~~my results support~~ the results of my study with native *P. australis* are consistent with the literature – competitive ability decreases with increasing latitude. Moreover, I also find support for the basic prediction ~~of~~ that invasive species (or genotypes) ~~increased competitive ability in invasive species as opposed to~~are better competitors than native species (Vila and Weiner 2004). More importantly, ~~However,~~ my study was the first to demonstrate that ~~also able to determine that variation in competitive ability between~~ native and invasive haplotypes ~~occurs over~~ exhibit non-parallel latitudinal gradients in competitive ability that potentially underlies geographic variation in invasion success. At northern latitudes~~e and as a result of size differences~~, the invasive haplotype is a far superior competitor against *S. alterniflora* than the native haplotypes. However, as latitude decreases, the competitive superiority of the invasive haplotype diminishes. Under these circumstances, invasion and spread of *P. australis* in northern latitudes may be more strongly facilitated by its competitive advantage over its neighbors. ~~thus areas susceptible to invasion occur in northern latitudes and/or are dominated by either the native haplotype of *P. australis* or *S. alterniflora*.~~ Additional research is needed ~~on multiple factors~~

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~~touched upon in this study,~~ to explore how the geographic origin of the invader and its site of invasion may affect competitive hierarchies and invasion success. ~~especially those such as low latitude (e.g. latitudes not covered in this study) native populations having increased competitive ability or species that may have the same niche as the invasive haplotype of *P. australis*. Forecasting the spread of the invasive haplotype of *P. australis* must now take account location invaded, and resident intraspecific competitors. Especially intriguing would be consideration of competitive ability of both the invasive and Gulf Coast haplotype over tropical latitudes.~~ Finally, this study strongly suggests that to understand the~~Regardless of the patterns found in this study, further research into~~ mechanisms governing the success of invasive species, they must accommodate a biogeographical approach.

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VITAE

Anthony Chow, was born in October of 1984 in Manhattan, New York. Although, if someone were to ask, he would answer that he was from Chicago. Regardless, it was not until he arrived in Knoxville, Tennessee that he found his love of ecology as an undergraduate student at the University of Tennessee-Knoxville. He spent a summer working in the lab of Dr. James Fordyce, studying the ecology of invasive species in the Great Smoky Mountains. During the following year, he worked in the lab of Dr. Jake Weltzin studying the effects of nitrogen and carbon enrichment on invasive species. Throughout his time as an undergraduate, Anthony went from wanting to study medicine to focusing on the interactions between species and the environment. Besides studying invasive species, Anthony also studied the community dynamics using a mesocosm-based approach.

After taking a year off to do voluntary research and teach undergraduate ecology labs, Anthony found himself in Baton Rouge, Louisiana as a graduate student at Louisiana State University in the lab of Dr. James Cronin. At LSU, Anthony's research have focused primarily on invasive species such as *Imperata cylindrica* (Cogongrass) and *Phragmites australis* (Common Reed). Before deciding to focus on how latitude affects competitive ability, he was interested in studying the production of allelopathic compounds by invasive species. Anthony's research will contribute further knowledge about invasive species and why they are such successful species. This new knowledge will hopefully be used to prevent further invasion of native systems by exotic species.