

Seed germination and seedling establishment of an invasive tropical tree species under different climate change scenarios

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Abstract Increasing air temperature and atmospheric CO₂ levels may affect the distribution of invasive species. Whereas there is wide knowledge on the effect of global change on temperate species, responses of tropical invasive species to these two global change drivers are largely unknown. We conducted a greenhouse experiment on *Terminalia catappa* L. (Combretaceae), an invasive tree species on Brazilian coastal areas, to evaluate the effects of increased air temperature and CO₂ concentration on seed germination and seedling growth on the island of Santa Catarina (Florianópolis, Brazil). Seeds of the invasive tree were subjected to two temperature levels (ambient and +1.6 °C) and two CO₂ levels (ambient and ~650 ppmv) with a factorial design. Increased temperature enhanced germination rate and shortened germination time of *T. catappa* seeds. It also increased plant height, number of leaves and above-ground biomass. By contrast, increased atmospheric CO₂ concentration had no significant effects, and the interaction between temperature and CO₂ concentration did not affect any of the measured traits. *Terminalia catappa* adapts to a relatively broad range of environmental conditions, being able to tolerate cooler temperatures in its invasive range. As *T. catappa* is native to tropical areas, global warming might favour its establishment along the coast of subtropical South America, while increased CO₂ levels seem not to have significant effects on seed germination or seedling growth.

Key words: CO₂ concentration, coastal dunes, establishment, invasive plant, plant invasion, temperature, *Terminalia catappa*.

INTRODUCTION

Climate change and biological invasions are expected to strongly affect biodiversity and ecosystem services worldwide (Schröter *et al.* 2005; Cardinale *et al.* 2012). Changes in climate may decrease ecosystem resistance to invasive species and enhance population growth of non-native species through several mechanisms. For instance, environmental changes can facilitate the spread of non-native species if native species are less competitive in terms of resource acquisition or ability to cope with biotic or abiotic stress factors (Qaderi *et al.* 2013; Manea *et al.* 2016). Although it is important to consider biological invasions in the light of climate change (Hellmann *et al.* 2008; Walther *et al.* 2009; Bradley *et al.* 2010), manipulative experiments have only occasionally addressed synergies among global change drivers (but see Jia

et al. 2016; Johnson & Hartley 2018). This may be especially the case of invasive species from tropical regions introduced to subtropical and temperate regions (Walther *et al.* 2009; Sheppard & Stanley 2014). Not surprisingly, our knowledge on invasion risk of tropical areas by alien tropical invaders is still scarce (Ackerman *et al.* 2017).

Several reports addressed the impact of increasing atmospheric CO₂ on the performance of invasive plant species compared with their native neighbours. Most of them reported an increase in biomass (Dukes 2002; Hättenschwiler & Körner 2003; Song *et al.* 2009) and height (Smith *et al.* 2000) of invasive species in the introduced range in response to higher CO₂ concentrations. The invasive species analysed included diverse growth forms ranging from annual grasses (Smith *et al.* 2000; Nagel *et al.* 2004) to shrubs (Hättenschwiler & Körner 2003; Belote *et al.* 2004), forbs (Dukes 2002) and perennial vines (Song *et al.* 2009). Evidence suggests that invasive plant species would overall benefit from higher

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atmospheric CO₂ levels (Bradley *et al.* 2010; Loveys *et al.* 2010), perhaps because of higher efficiency in gas exchange (Anderson & Cipollini 2013; de Faria *et al.* 2018).

Most expectations about the effect of increasing temperature on plant invaders are based on habitat-suitability models (Kriticos *et al.* 2003; Bradley *et al.* 2010; Qin *et al.* 2016; Bellard *et al.* 2018; Hannah *et al.* 2019). In an extensive revision on the effects of climate change on the potential spread of invasive, non-native species Bellard *et al.* (2018) reported that predictions for plants are scale-dependent. Whereas the range of invasive plants are more often predicted to decrease than to increase at large, continental scales the opposite is expected at regional or local scales (Bellard *et al.* 2018). In the lack of field manipulations, greenhouse experiments have shown that warming enhances seed germination and seedling growth of different invasive species (Wang *et al.* 2011; Hou *et al.* 2014; Skálová *et al.* 2015), although there are reports of negative impacts of global warming on germination and seedling establishment in temperate regions (e.g. Footitt *et al.* 2018). The impacts of global warming on seed and seedling responses have been relatively little addressed (Parmesan & Hanley 2015) despite being critical phases in which plants often suffer high mortality rates. These two critical, early life-history stages constitute the first hurdles of invasion success (Dechoum *et al.* 2015; Hirsch *et al.* 2016) in a complex process subject to multiple influences (Zenni *et al.* 2017).

Some reports have shown that elevated CO₂ levels enhance the effects of higher temperatures, increasing plant growth and biomass (e.g. Qaderi *et al.* 2013; de Faria *et al.* 2018), but evidence is scant and suggests that it may not be always the case (e.g. Hely & Roxburgh 2005). For instance, Sheppard and Stanley (2014) simulated current conditions and conditions projected for the end of the century using environmental chambers under two temperature (23.7 and 26 °C) and two CO₂ (450 and 900 ppmv) regimes, assessing the effects for seedling growth of three woody invasive species in New Zealand. They reported a significant interaction between increased temperature and doubled CO₂ level only for the relative growth rate of one of the species, without effects on the other two species or on other traits. As a matter of fact, although non-native plants of tropical and subtropical origins introduced to colder regions are expected to increase in population number and size and spread farther with climate change (Sheppard & Stanley 2014), evidence shows that the success of these invasions are species- and context-dependent (Walther *et al.* 2009).

Coastal sand dunes are the most frequently invaded habitats in Europe (Chytrý *et al.* 2008), and highly susceptible to invasions worldwide (Campos

et al. 2004; Defeo *et al.* 2009; Carboni *et al.* 2010; Barbosa *et al.* 2017) since they experience frequent disturbance and strong environmental stress (Castillo & Moreno-Casasola 1996; Davis *et al.* 2000). Island coastal communities are threatened by changes in climate (Harley *et al.* 2006) but, overall, by extreme weather events (Burgiel & Muir 2010) which remove large amounts of standing plant biomass and decrease the resistance of native communities to the establishment of invaders by decreasing the competitive ability of native species (Diez *et al.* 2012). In addition, urbanisation processes and tourism expansion over coastal areas facilitate the introduction of non-native species, mostly ornamental plants (Alston & Richardson 2006).

One expanding non-native species in coastal ecosystems is *Terminalia catappa* L. (Combretaceae), a tree species native to tropical regions in the Malaysian Peninsula, Southeast Asia and the Andaman Islands (CABI 2019). This species is invasive in coastal ecosystems in Brazil, with Florianópolis (Santa Catarina Island, Brazil) being so far the southernmost point of occurrence (I3N Brazil 2017). The climate in Florianópolis is subtropical (Cfa in the Köppen-Geiger classification), therefore different in temperature and precipitation from the native range of *T. catappa* (Am and Af in the Köppen-Geiger classification).

Assessing the effects of increased CO₂ levels on different life cycle stages is important to better understand its effects on plant performance in natural ecosystems. With this purpose, we carried out a greenhouse experiment to assess the synergistic effects of increased air temperature and CO₂ concentration on seed germination and seedling growth of the invasive tree species *Terminalia catappa*. Considering differences in temperature between the native range (tropical climate) of *T. catappa* and southern Brazil (subtropical climate), and the potential effects of elevated CO₂ on plant growth, we hypothesised that (i) warming, as a single factor, would enhance the germination rate of *T. catappa* seeds; (ii) *T. catappa* seedlings would show higher growth rates under increased levels of atmospheric CO₂. Finally, we expected (iii) a synergistic effect between temperature and CO₂ increases that would enhance *T. catappa* germination and seedling growth.

METHODS

Invasion by *Terminalia catappa*

The regional climate in Florianópolis is Cfa type – humid subtropical climate according to the Köppen-Geiger classification. The mean temperature ranges from 26 °C in summer to 16 °C in winter, with an annual mean of 20 °C (EMBRAPA 2017). Rainfall is well distributed

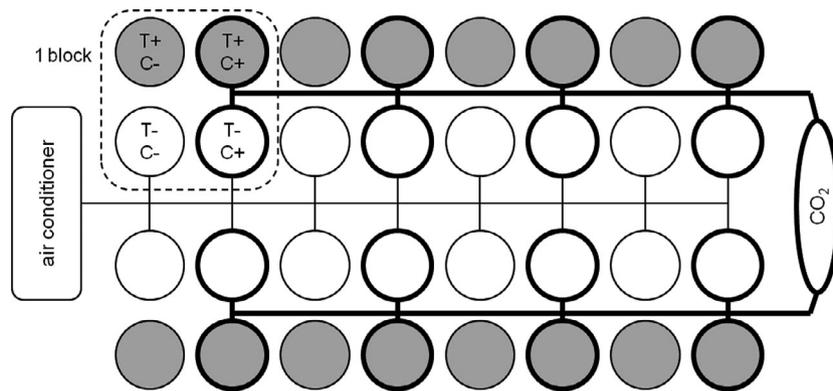


Fig. 1. Experimental design of the greenhouse experiment. We used 32 chambers (1 chamber = 1 tray with 6 *T. catappa* seeds) for 13 weeks combining increased air temperature (grey circles) and increased CO₂ level (clear circles). This resulted in 8 blocks comprising four treatments: T – C– (control, ambient temperature and CO₂ concentration); T – C+ (ambient temperature and increased CO₂ concentration); T + C– (increased temperature and ambient CO₂ concentration); and T + C+ (increased temperature and CO₂ concentration).

throughout the year, but higher in summer months, with an annual average of 1500 mm (EMBRAPA 2017).

The spread of *T. catappa* on coastal scrub (named *restinga* in Portuguese) has been documented in Florianópolis since 2009, with a significant increase in distribution between 2011 and 2013 (Plucênio *et al.* 2013). As seeds germinate and seedlings and juveniles grow in natural areas, some of them reaching the reproductive stage, the species is in the naturalisation phase of the invasion process (Richardson *et al.* 2000).

Experimental design

The experiment was carried out in a greenhouse at the Federal University of Santa Catarina (Florianópolis, southern Brazil) for 13 weeks between February and May 2016. We assessed the effects of increased air temperature and CO₂ concentration on seed germination and seedling growth of *T. catappa* in a greenhouse experiment with a factorial design. We established two levels for each of the two factors; increased (T+) and ambient temperature (T–); and increased (C+) and ambient CO₂ (C–). Therefore, we applied four treatments: control (T – C–), increased air temperature and ambient CO₂ concentration (T + C–), ambient air temperature and increased CO₂ concentration (T – C+), and increased air temperature and increased CO₂ concentration (T + C+). Our target was to increase temperature, on average, by 1.6 °C and CO₂ to 600–700 ppmv, as is expected for year 2100 (IPCC 2013; Magrin *et al.* 2014).

The experiment consisted of eight blocks, each including one replicate of each treatment (Fig. 1). Each experimental unit consisted of a plastic tray (30 × 45 cm) placed inside an acrylic chamber (AC; Fig. 1) used to increase air temperature. To increase CO₂ concentration in chambers (C+ treatments), we sealed ACs with transparent, self-adhesive film, leaving only the tray bottom open to allow percolation of excess water. Chambers in CO₂ control treatments (C–) were also sealed to avoid

experimental artifacts. As ACs increased air temperature in all experimental units, we had to cool down half the ACs to achieve ambient temperature in the ‘control’ treatments (T–). For this purpose, an air conditioning system was set up using a split air conditioner, and PVC tubes isolated with thermal blankets to cool off half the chambers. The other half were supplied with ambient air from outside the greenhouse through a piping system connected to a forced ventilation device.

CO₂ concentration was maintained in C+ treatments at ~600–700 ppmv (Table 1) using gas cylinders. An infrared sensor (LI-COR Biosciences, Lincoln, NE, USA) connected to the tank controlled the amount of gas released. Each experimental chamber was an independent, closed system with an entrance of fresh air (cooled or not), and half of them had an additional entrance for CO₂-enriched air (Appendix 1).

Fruits of *T. catappa* were collected from 20 different trees in *restinga* in Florianópolis at the end of autumn/early winter 2015 (June–August) and kept at 6 °C until the beginning of the experiment. The endocarp was removed to improve germination (Sanches 2009). Seeds were then

Table 1. Mean (±SD) of air temperature and CO₂ concentration in four treatments: T + C+ (increased temperature and CO₂ concentration), T + C– (increased temperature and ambient CO₂ concentration), T – C+ (ambient temperature and increased CO₂ concentration) and T – C– (control, ambient conditions)

Variable	Level	Treatment	Mean ± SD
Air temperature (°C)	T+	T + C+	25.4 ± 0.53
		T + C–	25.1 ± 0.84
	T–	T – C+	23.8 ± 1.12
		T – C–	23.5 ± 1.09
CO ₂ concentration (ppmv)	C+	T + C+	692 ± 36
		T – C+	570 ± 54
	C–	T + C–	384 ± 9
		T – C–	360 ± 8

sterilised in a 75% ethanol solution for two minutes to avoid fungal infection. Six *T. catappa* seeds were sown in each tray filled with vermiculite. Trays were watered frequently (approx. every 4 days), whenever vermiculite started to dry. Trays with increased air temperature (T+) were supplied ~450 mL water and trays at ambient air temperature (T-) with ~650 mL. The difference in watering was needed to account for the dehydrating effect of cooling by air conditioning, which could not be avoided, and was based on a daily monitoring of vermiculite. As soon as drying was noticed, the trays were watered.

Data collection

Temperatures were recorded hourly with iButton data loggers (Maxim Integrated, San Jose, CA, USA) installed inside each chamber. CO₂ concentration in the chambers was checked periodically with a portable IR sensor to maintain 600–700 ppmv in C+ treatments.

Terminalia catappa seed germination was recorded daily in all chambers. Seedling growth was measured weekly for a period of five weeks before the leaves were removed for analyses. All plants that germinated after the 8th week of the experiment were not considered for growth parameters but just recorded for seed germination analysis.

Plant height, number of leaves and plant mass (above and below ground) were measured and recorded for each *T. catappa* individual alive at the end of the experiment ($n = 76$). Specific leaf area (SLA) was determined by standard methods (Pérez-Harguindeguy *et al.* 2013). All the leaves of each seedling were removed, labelled and weighed with a precision scale. Then, each leaf was digitised with a scanner, oven-dried in paper bags at 72 °C for 48 h, and weighed. The projected areas of the scans were measured using Midebmp software (EEZA, Almería, Spain), and SLA was determined for each single leaf as a ratio between leaf area and dry mass. Mean SLA values were averaged for each seedling. The same procedure was followed in determining leaf dry matter content (LDMC). Above- and below-ground plant parts were sorted out after leaf removal, oven-dried at 72 °C for 48 h, and weighed with a precision balance to obtain dry mass. Data of seedlings per chamber were averaged prior to statistical analyses.

Statistical analyses

Records of CO₂ concentration and air temperature were averaged for each chamber. The Wilcoxon test was used to compare air temperature between T+ and T- treatments, while the *t*-test was used to test for differences in CO₂ concentration between C+ and C- treatments. The velocity of germination coefficient was calculated for each tray following Kader (2005). Differences between treatments regarding germination rate, velocity of germination, as well as performance estimators (plant height, number of leaves, above- and below-ground dry mass, SLA and LDMC) were analysed with linear mixed-effect models (GLMM) considering air temperature, CO₂ concentration and the interaction between them as fixed factors. Blocks were considered a random factor. Seedlings without leaves were not included in the models for SLA and LDMC ($n = 62$). All

statistical analyses were performed with the software R version 3.0.3 (R Core Team 2014), using the package 'lme4' (Bates *et al.* 2014) for the GLMMs, and 'sciplot' (Morales 2012) for the figures.

RESULTS

Chambers significantly increased air temperature ($W = 12, P < 0.001$), and T+ treatments were on average 1.6 °C warmer during the day than T- treatments (Table 1), but temperatures at night were similar. CO₂-enriched chambers (C+) had ~50% higher CO₂ concentration on average than ambient CO₂ (C-) chambers ($t = 13.1, d.f. = 16, P < 0.001$, Table 1).

Seed germination started 11 days after sowing. A total of 105 seeds germinated during the experiment, equivalent to 55% of the total sown. In the T + C+ treatment, 68.8% of seeds germinated along the course of the experiment, compared with 62.5% in T + C-, 47.9% in T - C+ and 39.6% in T - C-. Velocity of germination was 7.85 days in T + C+ (DP = ±3.06), 9.16 days (±6.09) in T + C-, 2.81 days (±0.45) in T - C+ and 2.48 days (±0.5) in T - C-. Hence, *T. catappa* seeds germinated notably slower in chambers with increased temperature ($Z = 2.23, P < 0.05$). By contrast, neither CO₂ increases nor the interaction CxT had any effect on velocity of germination ($Z = 0.82, P = 0.41$ for CO₂ and $Z = 0.10, P = 0.92$ for CxT, respectively; AIC: 118.7, Fig. 2). All differences were therefore due to

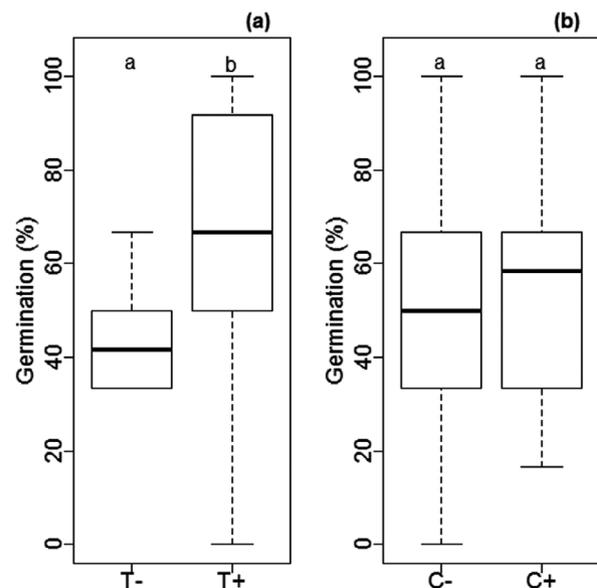


Fig. 2. Boxplot of *Terminalia catappa* seed germination rate at (a) ambient temperature (T-) and increased temperature (T+); and (b) ambient (C-) and increased CO₂ (C+) levels. Different letters mean significant differences in paired comparisons (T- and T+, and C- and C+).

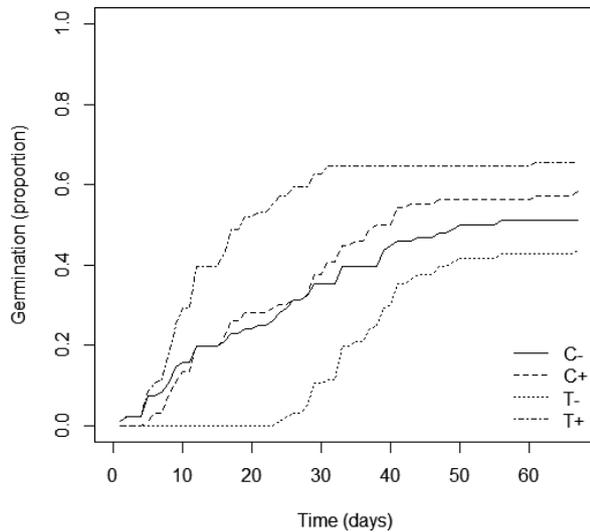


Fig. 3. Cumulative percentage of germination of *Terminalia catappa* seeds at ambient (T⁻) and increased (T⁺) temperature, and ambient (C⁻) and increased (C⁺) CO₂ levels.

temperature. In chambers with ambient temperature (T⁻ C⁺ and T⁻ C⁻) germination started three weeks later (Fig. 3), CO₂ had no effect ($t = 0.33$, $P = 0.74$) and the non-significant CxT interaction again suggest that all differences were due to temperature ($t = 0.44$, $P = 0.66$; AIC: 172.3, Fig. 3).

Temperature also affected plant growth and allocation patterns, increasing plant height, number of leaves and above-ground biomass (Table 2). It also led to a decrease in the root-to-shoot ratio, showing that plants in warmer temperature allocated less biomass to roots. Warming, however, had no effect on total biomass, SLA or LDMC (Table 2). Contrary to our expectations, CO₂ concentration did not have any effect on any seedling trait measured (Table 2).

Table 2. Morphological and functional traits (mean \pm SD) of *T. catappa* seedlings in the four treatments: T + C⁺ (increased temperature and CO₂), T + C⁻ (increased temperature and ambient CO₂), T⁻ C⁺ (ambient temperature and increased CO₂) and T⁻ C⁻ (control, ambient conditions). P values (T for the effect of temperature, CO₂ for the effect of CO₂ concentration and T \times CO₂ for the effect of the interaction between factors) and Akaike's Information Criterion (AIC) of the GLMMs are also presented. Units for height is cm, for biomass is g, for SLA m² kg⁻¹, and for LDMC mg g⁻¹. Significant P values are in bold

Treatment	Height	Number of leaves	Total biomass	Total above-ground biomass	Root-to-shoot ratio	SLA	LDMC
T + C ⁺	16.0 \pm 5.7	2.5 \pm 1.3	0.61 \pm 0.24	0.49 \pm 0.18	0.29 \pm 0.06	32.1 \pm 0.86	197 \pm 99
T + C ⁻	17.3 \pm 3.9	2.8 \pm 1.3	0.59 \pm 0.27	0.51 \pm 0.20	0.25 \pm 0.06	34.7 \pm 1.01	203 \pm 97
T ⁻ C ⁺	10.4 \pm 3.0	1.2 \pm 1.2	0.49 \pm 0.10	0.39 \pm 0.07	0.32 \pm 0.05	30.5 \pm 1.28	235 \pm 187
T ⁻ C ⁻	8.8 \pm 3.2	1.0 \pm 0.9	0.45 \pm 0.16	0.37 \pm 0.10	0.32 \pm 0.06	27.8 \pm 1.47	175 \pm 87
Statistics							
P (T)	<0.001	<0.01	0.07	<0.05	<0.01	0.23	0.46
P (CO ₂)	0.29	0.67	0.54	0.55	0.95	0.60	0.27
P (T \times CO ₂)	0.22	0.55	0.64	0.40	0.09	0.43	0.31
AIC	458.2	249.8	17.5	60.9	161	773.2	734

DISCUSSION

Increased temperature had positive effects on *T. catappa* seed germination and seedling growth, while increased CO₂ concentration had no effect. Therefore, our first hypothesis was supported, but not our two other hypotheses regarding the effect of CO₂ on seedling growth and the combined effect of temperature and CO₂ on seed germination and seedling growth. Our results showed that even a small rise in daytime temperature (1.6 °C) was enough to enhance the germination rate of *T. catappa* seeds. Pearson *et al.* (2002) reported that some tropical pioneer species, especially those with larger seeds, had increased germination rates with increasing temperature most likely due to its effects on seed coat permeability (Baskin & Baskin 1998). But temperature is also one of the main factors regulating seed physiology, influencing many metabolic processes relevant to seed dormancy and germination (Probert 2000), as well as traits relevant to plant establishment and performance (Walck *et al.* 2011).

Contrary to our expectations, *T. catappa* seedlings did not respond to increased CO₂ levels in terms of growth (height, biomass, number of leaves) or functional traits (root/shoot, SLA, LDMC). These results are not surprising, as similar outcomes have been reported elsewhere (Tooth & Leishman 2014; Manea *et al.* 2016). However, controversial results and predictions have been published showing a better performance of invasive species than of native species in elevated CO₂ conditions (Raizada *et al.* 2009; Bradley *et al.* 2010; Liu *et al.* 2017), indicating an increase in the spread of invasive plant species.

The lack of response by *T. catappa* to higher CO₂ levels could be due to the short-term focus of our experimental design, which may not have been maintained long enough. Norby *et al.* (1992) found that

growth efficiency (above-ground mass per unit leaf area) increased only after two years of CO₂ enrichment. Similarly, Hättenschwiler and Körner (2003) reported that increased CO₂ levels enhanced biomass production after three growing seasons in *Prunus laurocerasus*, an invasive shrub in temperate forests. In addition, increased water use efficiency is one potential benefit of elevated CO₂ (Allen *et al.* 2011; Cheng *et al.* 2017). However, this potential benefit was largely counteracted by our watering regime, one possible reason for the lack of response to higher CO₂ levels.

The combined effect of increased temperature and increased CO₂ on invaders has been scantily addressed in the scientific literature. Evidence is not strong enough to draw consistent conclusions. It has been shown, however, that both drivers combined weaken the positive effect of single factors on invasive herb species, as experimental warming may counteract any positive impacts of increased CO₂ alone (Williams *et al.* 2007; Van de Velde *et al.* 2015). However, Liu *et al.* (2017) reported that elevated temperature and CO₂ enrichment increased the performance of invasive alien plant species more strongly than that of native species. In other experiments, the combined effects of increased temperature and high CO₂ provided inconsistent results, suggesting that it is highly species-specific and context-dependent (Bradley *et al.* 2010; Huang 2016).

Terminalia catappa seedlings showed high phenotypic variability expressed through functional traits in response to temperature increase. This suggests a high tolerance range to temperature variation especially during early developmental stages when plants are most vulnerable. However, it is not clear how adult individuals of *T. catappa* will respond to these environmental changes and whether this variability is adaptive, resulting in greater fitness. As there are no native congeners to the invasive *T. catappa* in the studied ecosystem, we were not able to test whether *T. catappa* has a higher level of variability/plasticity than related native species. It is worth mentioning, though, that most studies addressing plasticity focused on species responses to resource availability and light (e.g. Funk 2008; Davidson *et al.* 2011; Godoy *et al.* 2011; Palacio-López & Gianoli 2011), while temperature has been somehow neglected in this context, which makes it difficult to place our results in a broader context.

In conclusion, our data show that the establishment of the invasive tree species, *Terminalia catappa*, will probably be favored in coastal scrub in southern Brazil, since seed germination and seedling growth were enhanced in conditions of increased air temperature. *Terminalia catappa* is able to adapt to a relatively broad range of environmental conditions, tolerating cooler temperatures in the invasive range.

With ongoing global warming trends, *T. catappa* might establish and spread to new areas. Thus, it is critical to identify areas susceptible to invasion, with particular attention to protected areas, and adopt appropriate prevention and control actions before invasions are consolidated. In addition, local regulations should be enforced to prevent the use of the species for ornamental purposes both in private and public properties. Actions must include the species control or eradication whenever possible on coastal areas to reduce propagule arrival on sites relevant for the conservation of biodiversity.

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APPENDIX 1



Picture of the experiment in the greenhouse, testing the effect of increases in temperature and CO₂ concentration on *Terminalia catappa* seed and seedling. Experimental units (closed chambers with trays filled with vermiculite) were supplied with ambient air and/or CO₂-enriched air (pipes in the middle of the bench), cooled air for ambient temperature provided by an air conditioner (silver isolated tubes) and with an output for air (yellow and orange tubes). *Terminalia catappa* seeds were sown in the 32 closed chambers and seedlings were harvested after a growth period of 6 weeks.