



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

Journal:	<i>Austral Ecology</i>
Manuscript ID	Draft
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Tietze, Hedwig Selma Eugenia; Universidade Federal de Santa Catarina, Programa de pós-graduação em Ecologia; Universitat Potsdam, Biodiversity Research/Systematic Botany, Institute of Biochemistry and Biology Joshi, Jasmin; Universitat Potsdam, Biodiversity Research/Systematic Botany, Institute of Biochemistry and Biology Pugnaire, Francisco; Estación Experimental de Zonas Áridas, CSIC , Ecología Funcional y Evolutiva; Dechoum, Michele; Federal University of Santa Catarina, of Ecology and Zoology
Keywords:	CO2 concentration, coastal dunes, establishment, invasive plant, plant invasion, Terminalia catappa, temperature

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

3

4 Hedwig Selma Eugenia Tietze^{1,2}, Jasmin Joshi^{2,4,5}, Francisco Ignacio Pugnaire³, Michele de
5 Sá Dechoum^{1*}

6

7 ¹ Programa de pós-graduação em Ecologia, Universidade Federal de Santa Catarina, Campus
8 Universitário s/n – Córrego Grande, Florianópolis, SC 88040-900, Brazil.

9 ² Biodiversity Research/Systematic Botany, Institute of Biochemistry and Biology, University
10 of Potsdam, Germany.

11 ³ Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas
12 (EEZA-CSIC), Ctra. Sacramento s/n, La Cañada, E-04120 Almería, Spain.

13 ⁴ Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin,
14 Germany, Altensteinstr. 6, 14195 Berlin, Germany.

15 ⁵ Hochschule für Technik HSR Rapperswil, Institute for Landscape and Open Space,
16 Seestrasse 10, 8640 Rapperswil, Switzerland

17 * Corresponding author: mdechoum@gmail.com; Telephone number: (+5548) 3304-2856

18

19 **Acknowledgements**

20 We thank Dr. Paulo Horta, Dr. Karla Scherer, Alexandre Schmidt and Lucas Machado
21 for assistance in the installation and maintenance of the experimental setup, and two
22 anonymous reviewers who provided valuable comments on an earlier draft of this manuscript.

23 This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível
24 Superior/Conselho Nacional de Desenvolvimento Científico e Tecnológico (CAPES/CNPq),
25 "Science without Borders" Program through the project "Plant interactions and community
26 dynamics in tropical, seasonal systems" (grant ref. UFSC 114A-2013). HT acknowledges

27 financial support of the University of Potsdam through the Promos scholarship of the
28 Deutscher Akademischer Austauschdienst (DAAD). FIP was recipient of a *Pesquisador*
29 *Visitante Especial* grant (CAPES/CNPq), and the support is gratefully acknowledged.

For Review Only

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

3

4 **Abstract**

5 Increasing air temperature and atmospheric CO₂ levels may affect the distribution of invasive
6 species. Whereas we have wide knowledge on the effect of global change on temperate
7 species, responses of tropical invasive species to these two global change drivers is largely
8 unknown. We used *Terminalia catappa* L. (Combretaceae), an invasive tree species in
9 Brazilian coastal areas, to address the effects of increased air temperature and CO₂
10 concentration on seed germination and seedling growth in a greenhouse experiment in the
11 Santa Catarina island (Florianópolis, Brazil). Seeds of the invasive tree species were subject
12 to two temperature levels (ambient and +1.6°C) and two CO₂ levels (ambient and ~650 ppm)
13 with a factorial design. Increased temperature enhanced germination rate and shortened
14 germination time of *T. catappa* seeds. It also increased plant height, number of leaves and
15 aboveground biomass. By contrast, increased atmospheric CO₂ concentration had no
16 significant effects, and the interaction between temperature and CO₂ concentration did not
17 affect any measured trait. *Terminalia catappa* adapts to a relatively broad range of
18 environmental conditions, being able to tolerate cooler temperatures in its invasive range.
19 Global warming might favour the establishment of *T. catappa*, a native to warmer tropical
20 regions, in South America coastal areas, while increased CO₂ levels seem not to have
21 significant effects on seed germination and seedling growth.

22

23 **Keywords:** CO₂ concentration; coastal dunes; establishment; invasive plant; plant invasion;
24 temperature; *Terminalia catappa*

25

26 **Introduction**

27 Climate change and biological invasions are expected to strongly affect biodiversity
28 and ecosystem services worldwide (Schröter et al. 2005; Cardinale et al. 2012). Changes in
29 climate may, through several mechanisms, decrease ecosystem resistance to invasive species
30 and enhance population growth of non-native species. For instance, environmental changes
31 can ease non-native species spread if native species are less competitive, in terms of resource
32 acquisition or in their ability to cope with biotic and abiotic stress factors (Qaderi et al. 2013,
33 Manea et al. 2016). Although it is important to consider biological invasions in the light of
34 climate change (Hellmann et al. 2008; Walther et al. 2009; Bradley et al. 2010) manipulative
35 experiments have only occasionally addressed synergies among global change drivers (but see
36 Jia et al. 2016; Johnson & Hartley 2018). This may be especially the case of invasive species
37 from tropical regions introduced to subtropical and temperate regions (Walther et al. 2009;
38 Sheppard et al. 2014). Not surprisingly, our knowledge on invasion risk of tropical areas by
39 alien tropical invaders is still scarce (Ackermann et al. 2017).

40 Several reports addressed the impact of increasing atmospheric CO₂ on the performance
41 of invasive plant species compared to their native neighbors. Most of them reported an
42 increase in biomass (Dukes 2002; Hättenschwiler & Körner 2003; Song et al. 2009) and
43 height (Smith et al. 2000) of invasive species in the introduced range in response to higher
44 CO₂ concentrations. The analyzed invasive species included growth forms ranging from
45 annual grasses (Smith et al. 2000; Nagel et al. 2004), to shrubs (Hättenschwiler & Körner
46 2003; Belote et al. 2004), forbs (Dukes 2002) or perennial vines (Song et al. 2009). Evidence
47 suggests that invasive plant species would overall benefit from higher atmospheric CO₂ levels
48 (Bradley et al. 2010; Loveys et al. 2010) perhaps because of higher gas exchange efficiency
49 (Anderson & Cipollini 2013; de Faria et al. 2018).

50 Most expectations about the effect of increasing temperature on plant invaders are based
51 on habitat-suitability models (Kriticos et al. 2003; Beaumont et al. 2009; McDonald et al.

52 2009; Bradley et al. 2010; Bellard et al. 2018). Lacking field manipulations, greenhouse
53 experiments have shown that warming enhances seed germination and seedling growth of
54 different invasive species (Hou et al. 2014; Skálová et al. 2015; Wang et al. 2011), although
55 there are reports of negative impacts of global warming on germination and seedling
56 establishment in temperate regions (e.g., Footitt et al. 2018). The impacts of global warming
57 on seed and seedling responses have been relatively little addressed (Parmesan & Hanley
58 2015), despite being critical phases which often suffer high mortality rates. These two critical,
59 early life-history stages constitute the first hurdles of invasion success (Dechoum et al. 2015;
60 Hirsch et al. 2016) in an otherwise complex process subject to multiple influences (Zenni et
61 al. 2017).

62 Some reports have shown that elevated CO₂ levels enhance the effects of higher
63 temperatures, increasing plant growth and biomass (e.g., Qaderi et al. 2013; de Faria et al.
64 2018), but evidence is scant and points that it may not be always the case (e.g., Hely &
65 Roxburgh 2005). For instance, Sheppard and Stanley (2014) simulated current conditions and
66 conditions projected for the end of the century using environmental chambers under the
67 combination of two temperature (23.7° and 26° C) and two CO₂ (450 and 900 ppmv)
68 regimes, assessing the effects for seedling growth of three woody invasive species in New
69 Zealand. They showed that a significant interactive effect of elevated temperature and
70 doubled CO₂ was observed only for the relative growth rate of the height of one of the
71 species, without any effects for the other two species or for other parameters such as total
72 biomass and total leaf area. As a matter of fact, although non-native plants of tropical and
73 subtropical origin introduced to colder regions are expected to increase the number and size of
74 their populations and spread farther with climate change (Sheppard & Stanley 2014),
75 evidence shows that the success of these invasions are species- and context-dependent
76 (Walther et al. 2009).

77 Coastal sand dunes are the most invaded habitats in Europe (Chytrý et al. 2008), and
78 highly susceptible to invasions worldwide (Campos et al. 2004; Defeo et al. 2009; Carboni et
79 al. 2010; Barbosa et al. 2017) since they experience frequent disturbances and strong
80 environmental stress (Castillo & Moreno-Casasola 1996; Davis et al. 2000). Island coastal
81 communities are threatened by changes in climate (Harley et al. 2006) but, overall, by
82 extreme weather events (Burgiel & Muir 2010) which remove large amounts of standing plant
83 biomass and decrease the resistance of native communities to the establishment of invaders by
84 decreasing the competitive ability of native species (Diez et al. 2012). In addition,
85 urbanization processes and tourism expansion over coastal areas facilitate the introduction of
86 alien species, mostly ornamentals (Alston & Richardson 2006).

87 One expanding alien species in a coastal environment is *Terminalia catappa* L.
88 (Combretaceae), a tree species native to Malaysia where average annual temperature is 27°C
89 (Tang 2012). This species is invasive in Brazil, especially in coastal ecosystems, with
90 Florianópolis (Santa Catarina, Brazil) being so far the southernmost point of occurrence (I3N
91 Brazil 2017). It is worth note that mean annual temperature in Florianópolis (20.3°C) is some
92 7°C lower than the native range of the species (EMBRAPA 2017).

93 Evaluating the effects of elevated CO₂ at different life cycle stages is important to
94 better understand its effects on whole-plant performance in natural ecosystems. With this
95 purpose, we carried out a greenhouse experiment to assess the synergistic effects of increased
96 air temperature and CO₂ concentration on seed germination and seedling growth of the
97 invasive tree species *Terminalia catappa*. Considering temperature differences between *T.*
98 *catappa* native range and southern Brazil, and the potential effects of elevated CO₂ on plant
99 growth, we hypothesized that 1) warming, as a single factor, would enhance germination rate
100 of *T. catappa* seeds; and 2) similarly, *T. catappa* seedlings would show higher growth rate
101 under increased levels of atmospheric CO₂. Finally, we expected 3) a synergistic effect

102 between temperature and CO₂ increases that would enhance *T. catappa* germination and
103 seedling growth.

104

105 **Methods**

106 *Experimental design*

107 In a greenhouse experiment with a factorial design, we assessed the effects of
108 increased air temperature and CO₂ concentration on seed germination and seedling growth of
109 *T. catappa*. We established two levels for each of the two factors; increased (T+) and ambient
110 temperature (T-); and increased (C+) and ambient CO₂ (C-). Therefore, we had four
111 treatments: control (T-C-), increased air temperature and ambient CO₂ concentration (T+C-),
112 ambient air temperature and increased CO₂ concentration (T-C+), and increased air
113 temperature and increased CO₂ concentration (T+C+). Our target was to increase temperature,
114 on average, by 1.6°C and CO₂ to 600-700 ppm, as expected for year 2100 (IPCC 2013;
115 Magrin et al. 2014). The experiment was carried out in a greenhouse at the Federal University
116 of Santa Catarina (Florianópolis, southern Brazil) for 13 weeks between February and May
117 2016.

118 The experiment consisted of eight blocks, each including one replicate of each
119 treatment (Fig. 1). Each experimental unit consisted of a plastic tray (30 x 45 cm) placed
120 inside an acrylic chamber (AC; Fig. 1) used to increase air temperature. To increase CO₂
121 concentration in chambers (C+ treatments), we sealed ACs with transparent, self-adhesive
122 film, leaving open only the tray bottom to allow percolation of excess water. Chambers in
123 CO₂ control treatments (C-) were also sealed to avoid experimental artifacts. As ACs
124 increased air temperature in all experimental units, we had to cool down half the ACs to
125 achieve ambient temperature in 'control' treatments (T-). For this purpose, we set up an air
126 conditioning system using a split air conditioner and PVC tubes isolated with thermal

127 blankets to cool off half the chambers. The other half was supplied with ambient air from
128 outside the greenhouse through a piping system connected to a forced ventilation device.

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

134 Fruits of *T. catappa* were collected at the Florianópolis coast at the end of
135 autumn/early winter 2015 (June–August) and kept at 6°C until the start of the experiment. We
136 removed the endocarp to improve germination (Sanches 2009). Seeds were then sterilized in a
137 75% ethanol solution for two minutes, to avoid fungal infection. Six *T. catappa* seeds were
138 sown in each tray, which were filled with vermiculite. Trays were watered frequently (aprox.
139 every 4 days), whenever vermiculite started to dry. Trays with increased air temperature (T+)
140 were supplied ~450 ml and trays at ambient air temperature (T-) with ~650 ml. The difference
141 in watering was needed to account for the dehydrating effect of cooling by air conditioning,
142 which could not be avoided.

143

144 *Data collection*

145 Temperatures were recorded hourly with iButton data loggers (Maxim Integrated, San
146 Jose, CA, USA) installed in the inner side of each chamber. CO₂ concentration in chambers
147 was checked periodically with a portable IR sensor to maintain a value of 600–700 ppm in C+
148 treatments.

149 Seed germination of *T. catappa* was recorded daily in all chambers. Seedling growth
150 was measured weekly for a period of five weeks before harvest. All plants that germinated
151 after the 8th week of the experiment were not considered for growth parameters but just
152 recorded for seed germination analysis.

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

165

166 *Statistical analyses*

167 Records of CO₂ concentration and air temperature were averaged for each chamber.
168 Wilcoxon test was used to compare air temperature between T+ and T- treatments, while t-
169 test was used to test for differences in CO₂ concentration between C+ and C- treatments. The
170 velocity of germination coefficient was calculated for each tray following Kader (2005).
171 Differences between treatments regarding germination rate, velocity of germination, as well
172 as performance estimators (plant height, number of leaves, above and belowground dry mass,
173 SLA and LDMC) were analyzed with linear mixed-effect models (GLMM) considering air
174 temperature, CO₂ concentration and the interaction between them as fixed factors. Blocks
175 were considered a random factor. Seedlings without leaves were not included in the models
176 for SLA and LDMC (n = 62). All statistical analyses were performed with the software R
177 version 3.0.3 (R Core Team 2014), using the package “lme4” (Bates et al. 2014) for the
178 GLMMs, and “sciplot” (Morales 2012) for the figures.

179

180 Results

181 Chambers significantly increased air temperature ($W = 12$, $p < 0.001$), and T+
182 treatments were on average 1.6°C warmer during daylight time than T- treatments (Table 1),
183 but temperatures at night were similar. CO_2 -enriched chambers (C+) had on average $\sim 50\%$
184 higher CO_2 concentration than ambient CO_2 (C-) chambers ($t = 13.1$, $\text{d.f.} = 16$, $p < 0.001$,
185 Table 1).

186 Seed germination started 11 days after sowing. A total of 105 seeds germinated during
187 the experiment, or 55% of the total seeds sown. In the T+C+ treatment, 68.8% of seeds
188 germinated along the course of the experiment, compared with 62.5% in T+C-, 47.9% in T-
189 C+ and 39.6% in T-C-. Hence, seeds of *T. catappa* germinated notably faster in chambers
190 with increased temperature ($Z = 2.23$, $p < 0.05$). By contrast, neither CO_2 increases nor the
191 interaction $\text{CO}_2 \times$ temperature did have any effect ($Z = 0.82$, $p = 0.41$ for CO_2 and $Z = 0.10$, p
192 $= 0.92$, respectively; AIC: 118.7, Fig. 2) pointing that all differences were due to temperature.
193 In chambers with ambient temperature (T-C+ and T-C-) germination started three weeks later
194 (Fig. 3) but CO_2 had no effect ($t = 0.33$, $p = 0.74$) and the non-significant T \times CO_2 interaction
195 again suggest all differences were due to temperature ($t = 0.44$, $p = 0.66$; AIC: 172.3, Fig. 3).

196 Temperature did also affect plant growth and allocation patterns, increasing plant
197 height, number of leaves, and aboveground biomass (Table 2). It also led to a decrease in the
198 root-to-shoot ratio, showing that warmed plants allocated less biomass to roots. Warming,
199 however, had no effect on total biomass, SLA or LDMC (Table 2). Contrary to our
200 expectations, CO_2 concentration did not have any effect on any seedling trait we measured
201 (Table 2).

202

203 Discussion

204 Increased temperature had positive effects on *T. catappa* seed germination and
205 seedling growth, while increased CO₂ concentration had no effects. Therefore, our hypotheses
206 were supported just in part. Our results showed that even a small rise in daytime temperature
207 (1.6°C) was enough to enhance *T. catappa* seed germination rate. Pearson et al. (2002)
208 reported that some tropical pioneer species, especially those with larger seeds, increased
209 germination rate with increasing temperature most likely due to its effects on seed coat
210 permeability (Baskin & Baskin 1998).

211 Contrary to our expectations, *T. catappa* seedlings did not respond to increased CO₂
212 levels, neither in terms of growth (height, biomass, number of leaves) or functional traits
213 (root/shoot, SLA, LDMC). These results are not surprising since similar outcomes have been
214 reported elsewhere (Tooth & Leishman 2014; Manea et al. 2016). However, controversial
215 results and predictions have been published showing a better performance of invasive species
216 when compared to native species under elevated CO₂ levels (Raizada et al. 2009; Bradley et
217 al. 2010; Liu et al. 2017), increasing the spread of invasive plant species.

218 The lack of responses to increased CO₂ in our species could be due to the short-term
219 focus of our experimental design, which may have not been long enough to induce responses.
220 Norby et al. (1992) found that growth efficiency (aboveground mass per unit leaf area)
221 increased only after two years of CO₂ enrichment. Similarly, Hättenschwiler and Körner
222 (2003) reported that increased CO₂ levels enhanced biomass production after three growing
223 seasons in *Prunus laurocerasus*, an invasive shrub in temperate forests. In addition, increased
224 water use efficiency is one potential benefit of elevated CO₂ (Allen Jr et al. 2011; Cheng et al.
225 2017). However, this potential benefit was largely eliminated by the watering regime, one
226 possible reason that a CO₂ effect was not observed.

227 The combined effect of increased temperature and increased CO₂ on invaders has been
228 scanty addressed in the scientific literature, and evidence is not strong enough to draw
229 consistent conclusions. It has been shown, however, that both drivers combined weaken the

230 positive effect of single factors on invasive herb species, as experimental warming may
231 counter any positive impacts of increased CO₂ alone (Williams et al. 2007; Van de Velde et
232 al. 2015). However, Liu et al. (2017) reported that elevated temperature and CO₂ enrichment
233 increased the performance of invasive alien plant species more strongly than of native species.
234 In other experiments, the combined effects of increased temperature and high CO₂ provided
235 inconsistent results, suggesting that it is highly species-specific and context-dependent
236 (Bradley et al. 2010; Huang 2016).

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

248 In conclusion, our data show that establishment of the invasive tree species,
249 *Terminalia catappa*, will probably be favored in coastal dunes of southern Brazil, since seed
250 germination and seedling growth were enhanced under increased air temperature. *Terminalia*
251 *catappa* is able to adapt to a relatively broad range of environmental conditions tolerating
252 cooler temperatures in the invasive range. With ongoing global warming trends, *T. catappa* is
253 expected to establish and spread into new areas. Thus, it is critical to identify areas
254 susceptible to invasion, with particular attention to protected areas, and adopt appropriate
255 control actions. In addition, local regulations should be enforced to prevent the use of the

256 species for ornamental purposes both in private and public properties. Actions should include
257 the species control and eradication when possible in coastal areas to reduce propagule arrival
258 in relevant sites for biological conservation.

259

260 **References**

- 261 Ackerman, JD; RL Tremblay; J Rojas-Sandoval; E Hernandez-Figueroa. 2017. Biotic
262 resistance in the tropics: patterns of seed plant invasions within an island. *Biol Invasions*
263 **19**:315–328
- 264 Allen, LH, Jr; VG Kakani; JC Vu; KJ Boote. 2011. Elevated CO₂ increases water use
265 efficiency by sustaining photosynthesis of water-limited maize and sorghum. *J Plant*
266 *Physiol* **168**(16):1909-18
- 267 Alston, KP & DM Richardson. 2006. The roles of habitat features, disturbance, and distance
268 from putative source populations in structuring alien plant invasions at the
269 urban/wildland interface on the Cape Peninsula, South Africa. *Biol Conserv* **132**:183–198
- 270 Anderson, LJ & D Cipollini. 2013. Gas exchange, growth, and defense responses of invasive
271 *Alliaria petiolata* (Brassicaceae) and native *Geum vernum* (Rosaceae) to elevated
272 atmospheric CO₂ and warm spring temperatures. *Am J Bot* **100**:1544-1554
- 273 Barbosa, C; MS Dechoum; TT Castellani. 2017. Population structure and growth of a non
274 native invasive clonal plant on coastal dunes in Southern Brazil. *Neotrop Biol Conserv*
275 **12**:214–223
- 276 Baskin, CC & JM Baskin. 1998. Seeds: Ecology, biogeography, and evolution of dormancy
277 and germination. Academic Press [San Diego, USA. 666 pp.]
- 278 Bates, D; M Maechler; B Bolker; S Walker. 2014. lme4: Linear mixed-effects models using
279 Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
280 Accessed 16 November 2016

- 281 Beaumont, LJ; RV Gallagher; W Thuiller; PO Downey; MR Leishman et al. 2009. Different
282 climatic envelopes among invasive populations may lead to underestimations of current
283 and future biological invasions. *Divers Distrib* **15**:409–420
- 284 Bellard, C; JM Jeschke; B Leroy; GM Mace. 2018. Insights from modeling studies on how
285 climate change affects invasive alien species geography. *Ecol Evol* **8**:5688–5700
- 286 Belote, RT; JF Weltzin; RJ Norby. 2004. Response of an understory plant community to
287 elevated [CO₂] depends on differential responses of dominant invasive species and is
288 mediated by soil water availability. *New Phytol* **161**:827–835
- 289 Bradley, BA; DM Blumenthal; DS Wilcove; LH Ziska. 2010. Predicting plant invasion in an
290 era of global change. *Trends Ecol Evol* **25**:310-318
- 291 Burgiel, SW & AA Muir. 2010. Invasive Species, Climate Change and Ecosystem-Based
292 Adaptation: Addressing Multiple Drivers of Global Change. *Global Invasive Species*
293 *Programme (GISP)* [Washington DC, USA & Nairobi, Kenya]
- 294 Campos, JA; M Herrera; I Biurrun; J Loidi. 2004. The role of alien plants in the natural
295 coastal vegetation in central-northern Spain. *Biodiv Conserv* **13**:2275–2293
- 296 Carboni, M; R Santoro; ATR Acosta. 2010. Are some communities of the coastal dune
297 zonation more susceptible to alien plant invasion? *J Plant Ecol* **3**:139–147
- 298 Cardinale, BJ; JE Duffy; A Gonzalez; DU Hooper; P Charles et al. 2012. Biodiversity loss
299 and its impact on humanity. *Nat* **486**:59–67
- 300 Castillo, SA & P Moreno-Casasola. 1996. Coastal sand dune vegetation: An extreme case of
301 species invasion. *J Coast Conserv* **2**:13–22
- 302 Cheng, L; L Zhang; Y-P Wang; JG Canadell; FHS Chiew et al. 2017. Recent increases in
303 terrestrial carbon uptake at little cost to the water cycle. *Nat Comm* **8**
- 304 Chytrý, M; LC Maskell; J Pino; P Pysek; M Villa et al. 2008. Habitat invasions by alien
305 plants: A quantitative comparison among mediterranean, subcontinental and oceanic
306 regions of Europe. *J Appl Ecol* **45**:448–458

- 307 Davidson, AM; M Jennions; AB Nicotra. 2011. Do invasive species show higher phenotypic
308 plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol Lett* **14**:419-
309 431
- 310 Davis, MA; JP Grime; K Thompson. 2000. Fluctuating resources in plant communities: A
311 general theory of invasibility. *J Ecol* **88**:528–534
- 312 Dechoum, MS; RD Zenni; TT Castellani; SM Zalba; M Rejmánek. 2015. Invasions across
313 secondary forest successional stages: effects of local plant community, soil, litter, and
314 herbivory on *Hovenia dulcis* seed germination and seedling establishment. *Plant Ecol*
315 **216**: 823-833
- 316 Defeo, O; A McLachlan; DS Schoeman; TA Schlacher; J Dugan et al. 2009. Threats to sandy
317 beach ecosystems: A review. *Estuar Coast Shelf Sci* **81**:1-12
- 318 Diez, JM; CM D'Antonio; JS Dukes; ED Grosholz; JD Olden et al. 2012. Will extreme
319 climatic events facilitate biological invasions? *Front Ecol Environ* **10**:249–257
- 320 Dukes, JS. 2002. Comparison of the effect of elevated CO₂ on an invasive species (*Centaurea*
321 *solstitialis*) in monoculture and community settings. *Plant Ecol* **160**:225–234
- 322 EMBRAPA – Empresa brasileira de pesquisa agropecuária. 2017. *Banco de dados climáticos*
323 *do Brasil*.
324 <https://www.cnpm.embrapa.br/projetos/bdclima/balanco/resultados/sc/231/balanco.html>.
325 Accessed 15 March 2017
- 326 de Faria, AP; MA Marabesi; M Gaspar; MGC Franca. 2018. The increase of current
327 atmospheric CO₂ and temperature can benefit leaf gas exchanges, carbohydrate content
328 and growth in C₄ grass invaders of the Cerrado biome. *Plant Physiol Biochem* **127**:608-
329 616
- 330 Footitt, S; Z Huang; H Olcer-Footitt; H Clay; WE Finch-Savage. 2018. The impact of global
331 warming on germination and seedling emergence in *Alliaria petiolata*, a woodland
332 species with dormancy loss dependent on low temperature. *Plant Biol* **20**:682–690

- 333 Funk, JL. 2008. Differences in p 381 lasticity between invasive and native plants from a low
334 resource environment. *J Ecol* **96**:1162–1173
- 335 Godoy, O; F Valladares; P Castro-Diez. 2011. Multispecies comparison reveals that invasive
336 and native plants differ in their traits but not in their plasticity. *Funct Ecol* **25**:1248–1259
- 337 Harley, CDG; AR Hughes; KM Hultgren; BG Miner; CJB Sorte et al. 2006. The impacts of
338 climate change in costal marine systems. *Ecol Lett* **8**:228–241
- 339 Hättenschwiler, S; C Körner. 2003. Does elevated CO2 facilitate naturalization of the non
340 indigenous *Prunus laurocerasus* in Swiss temperate forests? *Funct Ecol* **17**:778–785
- 341 Hellmann, JJ; JE Byers; BG Bierwagen; JS Dukes. 2008. Five potential consequences of
342 climate change for invasive species. *Conserv Biol* **22**:534–543
- 343 Hely, SEL; SH Roxburgh. 2005. The interactive effects of elevated CO2, temperature and
344 initial size on growth and competition between a native C3 and an invasive C3 grass.
345 *Plant Ecol* **177**:85–98
- 346 Hirsch, H; I Hensen; K Wesche; D Renison; C Wypior et al. 2016. Non-native populations of
347 an invasive tree outperform their native conspecifics. *AoB Plant* **8**:plw071
- 348 Hou, QQ; BM Chen; SL Peng; LY Chen. 2014. Effects of extreme temperature on seedling
349 establishment of nonnative invasive plants. *Biol Invasions* **16**:2049–2061
- 350 Huang, G. 2016. *Differential response to climate change among populations for woody plant*
351 *species: An ecological and physiological approach*. PhD thesis, Western Sydney
352 University [Australia]
- 353 I3N Brazil. 2017. *National database on invasive alien species – I3N Brasil*.
354 <http://i3n.institutohorus.org.br>. Accessed 01 February 2017
- 355 IPCC. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working*
356 *Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate*
357 *Change in: TF Stocker; D Qin; G-K Plattner; M Tignor; SK Allen et al. (eds). Cambridge*
358 *University Press [Cambridge, United Kingdom & New York, USA. 1585 pp.]*

- 359 Jia, JJ; ZC Dai; F Li; YJ Liu. 2016. How will global environmental changes affect the growth
360 of alien plants? *Front Plant Sci* **7**:1623
- 361 Johnson, SN; SE Hartley. 2018. Elevated carbon dioxide and warming impact silicon and
362 phenolic-based defences differently in native and exotic grasses. *Glob Change Biol* **24**:
363 3886-3896
- 364 Kader, MA. 2005. A comparison of seed germination and calculation formulae and the
365 associated interpretation of resulting data. *J Proc R Soc New South Wales* **138**:65–75
- 366 Kriticos, DL; RW Sutherst; JR Brown; SW Adkins; GF Maywald. 2003. Climate change and
367 the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in
368 Australia. *J Appl Ecol* **40**:111–124
- 369 Liu, YJ; AMO Oduor; Z Zhang; A Manea; IM Tooth et al. 2017. Do invasive alien plants
370 benefit more from global environmental change than native plants? *Global Change Biol*
371 **23**:3363-3370
- 372 Loveys, BR; JIG Egerton; D Bruhn; MC Ball. 2010. Disturbance is required for CO₂-
373 dependent promotion of woody plant growth in grasslands. *Funct Plant Biol* **37**:555-565
- 374 Magrin, GO; JA Marengo; J-P Boulanger; MS Buckeridge; E Castellanos et al. 2014. Central
375 and South America. [27] Pp. 1499-1566 in: VR Barros; CB Field; DL Dokken; MD
376 Mastrandrea; KL Mach et al. (eds). *Climate Change 2014: Impacts, Adaptation, and*
377 *Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth*
378 *Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge
379 University Press [Cambridge, USA. 1585 pp.]
- 380 Manea, A; DR Sloane; MR Leishman. 2016. Reductions in native grass biomass associated
381 with drought facilitates the invasion of an exotic grass into a model grassland system.
382 *Oecol* **181**:175–183

- 383 McDonald, A; S Riha; A Ditommaso; A Degaetane. 2009. Climate change and the geography
384 of weed damage: Analysis of US maize systems suggest the potential for significant
385 range transformations. *Agric Ecosyst Environ* **130**:131–140
- 386 Morales, M. 2012. *sciplot*: Scientific 431 graphic functions for factorial designs. R package
387 version 1.1-0. <http://CRAN.R-project.org/package=sciplot>. Accessed 20 April 2017
- 388 Nagel, JM; TE Huxman; KL Griffin, SD Smith. 2004. CO₂ enrichment reduces the energetic
389 cost of biomass construction in an invasive desert grass. *Ecol* **85**:100–106
- 390 Norby, RJ; CA Gunderson; SD Wullschleger; EG O'Neill; MK McCracken. 1992.
391 Productivity and compensatory response of yellow poplar trees in elevated CO₂. *Nat*
392 **357**:322–324
- 393 Palacio-López, K; E Gianoli. 2011. Invasive plants do not display greater phenotypic
394 plasticity than their native or non-invasive counterparts: A meta-analysis. *Oikos*
395 **120**:1393– 1401
- 396 Parmesan, C; ME Hanley. 2015. Plants and climate change: complexities and
397 surprises. *Annals of Botany*, **116**:849–864
- 398 Pearson, TRH; DFRP Burslem; SE Mullins; JW Dalling. 2002. Germination ecology of
399 neotropical pioneers: Interacting effects of environmental conditions and seed size. *Ecol*
400 **83**:2798–2807
- 401 Pérez-Harguindeguy, N; S Diaz; E Garnier; S Lavorel, H Poorter et al. 2013. New handbook
402 for standardized measurement of plant functional traits worldwide. *Aust J Bot* **61**:167-234
- 403 Qaderi, MM; AL Lynch; VJ Godin; DM Reid. 2013. Single and interactive effects of
404 temperature, carbon dioxide and watering regime on invasive weed black knapweed
405 (*Centaurea nigra*). *Ecosciences* **20**:328–338
- 406 R Core Team. 2014. R: A language and environment for statistical computing. R Foundation
407 for Statistical Computing. [Vienna] <http://www.R-project.org/>

- 408 Raizada, P; A Singh; AS Raghubanshi. 2009. Comparative response of seedlings of selected
409 native dry tropical and alien invasive species to CO₂ enrichment. *J Plant Ecol* **2**(2):69-75
- 410 Sanches, JH. 2009. *Potencial invasor do chapéu-de-sol (Terminalia catappa L.) em área de*
411 *restinga*. Master thesis, University of São Paulo [Brazil].
- 412 Schröter, D; W Cramer; R Leemans; IC Prentice; M-B Araújo et al. 2005. Ecosystem service
413 supply and vulnerability to global change in Europe. *Sci* **310**:1333–1337
- 414 Sheppard, CS; MC Stanley. 2014. Does elevated temperature and doubled CO₂ increase
415 growth of three potentially invasive plants? *Invasive Plant Sci Manag* **7**: 237-246
- 416 Skálová, H; L Moravcová; AFG Dixon; P Kindlmann; P Pysek. 2015. Effect of temperature
417 and nutrients on the growth and development of seedlings of an invasive plant. *AoB Plant*
418 **7**:plv074
- 419 Smith, SD; TE Huxman; SF Zitzer; TN Charlet; DC Housman et al. 2000. Elevated CO₂
420 increases productivity and invasive species success in an arid ecosystem. *Nat* **408**:79–82
- 421 Song, LY; J Wu; C Li; F Li; S Peng et al. 2009. Different responses of invasive and native
422 species to elevated CO₂ concentration. *Acta Oecol* **35**:128–135
- 423 Tang, CK. 2012. Malaysia's weather data. Building energy efficiency technical guideline for
424 passive design. [2] in: CK Tang; L Chin (eds). *Building sector energy efficiency project*.
425 [http://bseep.weebly.com/uploads/8/0/7/2/8072374/chapter_2_-](http://bseep.weebly.com/uploads/8/0/7/2/8072374/chapter_2_-_malaysia_weather_data_draft_01.pdf)
426 [_malaysia_weather_data_draft_01.pdf](http://bseep.weebly.com/uploads/8/0/7/2/8072374/chapter_2_-_malaysia_weather_data_draft_01.pdf).
- 427 Tooth, IM; M Leishman. 2014. Elevated carbon dioxide and fire reduce biomass of native
428 grass species when grown in competition with invasive exotic grasses in a savanna
429 experimental system. *Biol Invasions* **16**:257-268
- 430 Van de Velde, H; D Bonte; H Abdelgawad; H Asard; I Nijs. 2015. Combined elevated CO₂
431 and climate warming induces effects of drought in *Lolium perenne* and *Plantago*
432 *lanceolata*. *Plant Ecol* **216**:1047–1059

- 433 Walther, G-R; A Roques; PE Hulme; MT Sykes; P Pysek et al. 2009. Alien species in a
434 warmer world: Risks and opportunities. *Trends Ecol Evol* **24**:686–693
- 435 Wang, RL; RS Zeng; SL Peng; BM Chen; XT Liang et al. 2011. Elevated temperature may
436 accelerate invasive expansion of the liana plant *Ipomoea cairica*. *Weed Res* **51**:574–580
- 437 Williams, AL; KE Wills; JK Janes; JK Vander Schoor, PCD Newton et al. 2007. Warming
438 free-air CO₂ enrichment alter demographics in four co-occurring grassland species. *New*
439 *Phytol* **176**:365–374
- 440 Zenni, RD; IA Dickie; MJ Wingfield; H Hirsch; CJ Crous et al. 2017. Evolutionary dynamics
441 of tree invasions: Complementing the unified framework for biological invasions. *AoB*
442 *Plant* **9**:plw085

443 **Table 1** Mean (\pm SD) of air temperature and CO₂ concentration in four treatments: T+C+
 444 (increased temperature and CO₂ concentration), T+C- (increased temperature and ambient CO₂
 445 concentration), T-C+ (ambient temperature and increased CO₂ concentration) and T-C-
 446 (control, ambient conditions).

Variable	Level	Treatment	Mean \pm SD
Air temperature (°C)	T+	T+C+	25.4 \pm 0.53
		T+C-	25.1 \pm 0.84
	T-	T-C+	23.8 \pm 1.12
		T-C-	23.5 \pm 1.09
CO₂ concentration (ppm)	C+	T+C+	692 \pm 36
		T-C+	570 \pm 54
	C-	T+C-	384 \pm 9
		T-C-	360 \pm 8

447

448 **Table 2** Morphological and functional traits (mean \pm SD) of *T. catappa* seedlings in the four treatments: T+C+ (increased temperature and CO₂),
 449 T+C- (increased temperature and ambient CO₂), T-C+ (ambient temperature and increased CO₂) and T-C- (control, ambient conditions). *p* values (T
 450 for the effect of temperature, CO₂ for the effect of CO₂ concentration and T x CO₂ for the effect of the interaction between factors) and Akaike's
 451 Information Criterion (AIC) of the GLMMs are also presented. Units for height is cm, for biomass is g, for SLA m²/kg, and for LDMC mg/g.
 452 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 (CO₂)	0.29	0.67	0.54	0.55	0.95	0.60	0.27
p (T x CO₂)	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
------------	-------	-------	------	------	-----	-------	-----

453

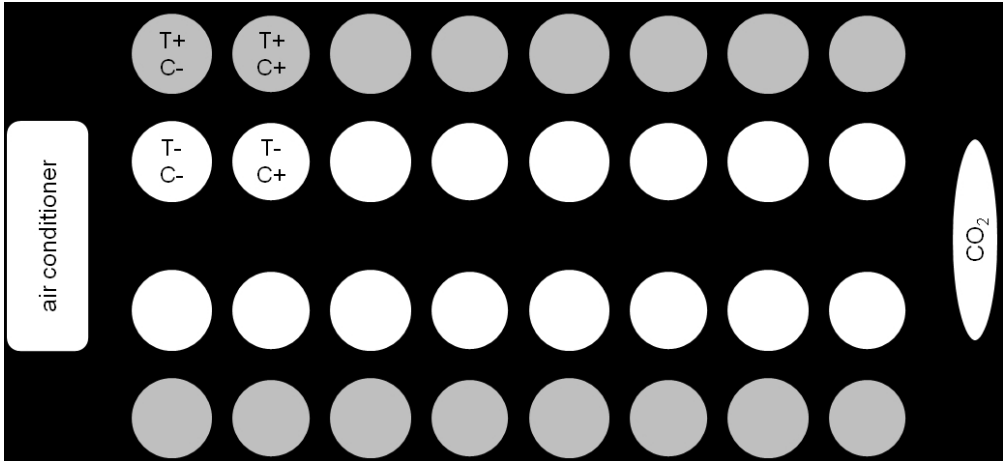
454

For Review Only

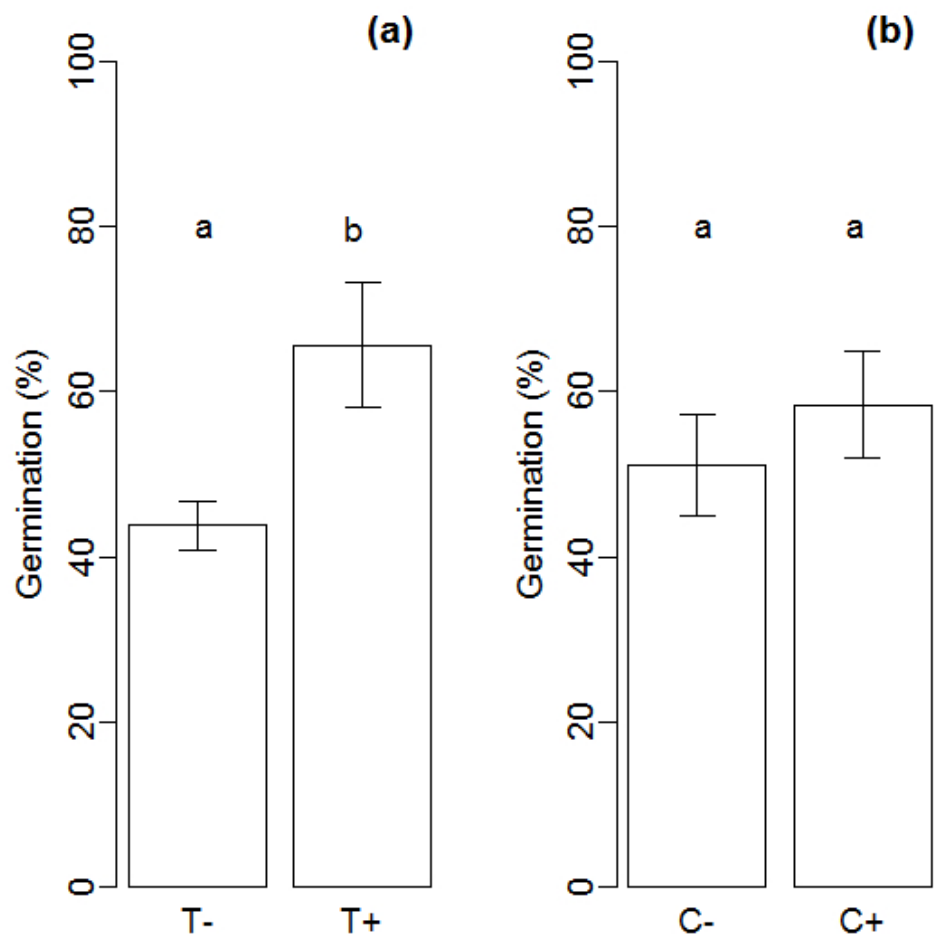
Fig. 1 Experimental design of the greenhouse experiment. We used 32 chambers (1 chamber = 1 tray with 6 *T. catappa* seeds) for 13 weeks combining increased air temperature (grey circles) and increased CO₂ level (clear circles). This resulted in 8 blocks comprising four treatments: T-C- (control, ambient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

Fig. 2 Percentage of germination (mean \pm SD) of *Terminalia catappa* seeds 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+).

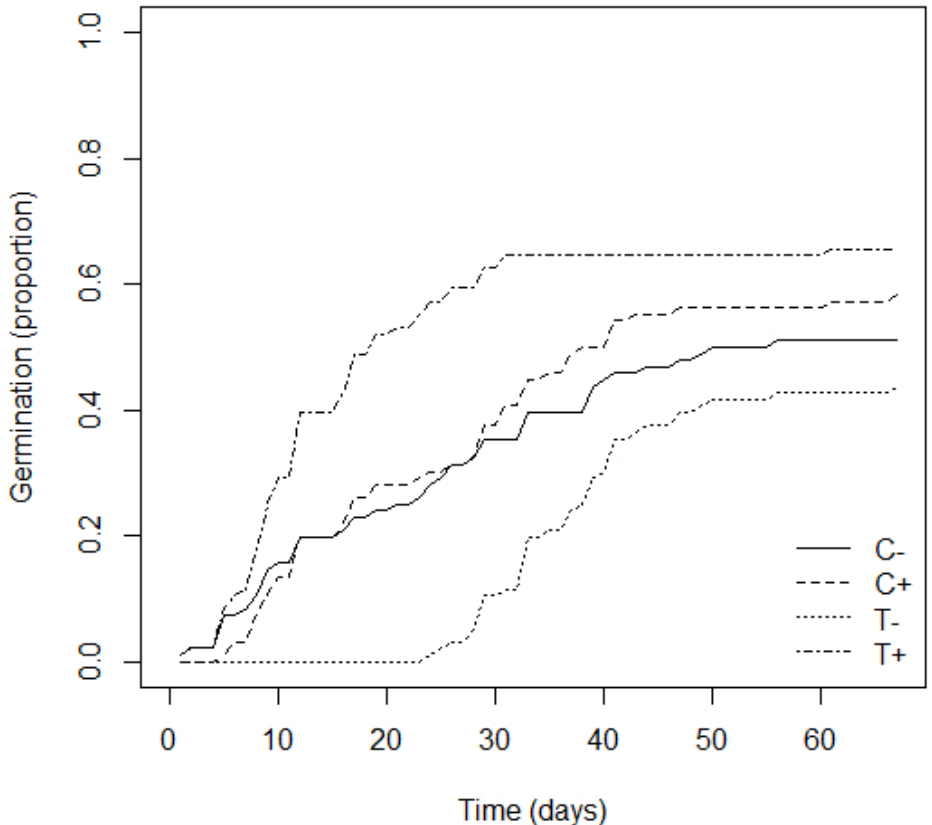
Fig. 3 Cumulative percentage of germination of *Terminalia catappa* seeds at ambient (T-) and increased (T+) temperature, and ambient (C-) and increased (C+) CO₂ levels.



175x80mm (150 x 150 DPI)



195x194mm (72 x 72 DPI)



195x194mm (72 x 72 DPI)

Appendix 1



Picture of the experiment in the greenhouse, testing the effect of increases in temperature and CO_2 concentration on *T. catappa* seed and seedling. Experimental units (closed chambers with trays filled with vermiculite) were supplied with ambient air and/or CO_2 -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). *T. catappa* seeds were sown in the 32 closed chambers and seedlings were harvested after a growth period of six weeks.