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
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 is 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 (Díez 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).

Experimental design

The experiment was carried out in a greenhouse at the Federal University of Santa Catarina (Florianopolis, 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 Florianopolis 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)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Level</th>
<th>Treatment</th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (°C)</td>
<td>T+</td>
<td>T + C+</td>
<td>25.4 ± 0.53</td>
</tr>
<tr>
<td></td>
<td>T+C</td>
<td>T + C–</td>
<td>25.1 ± 0.84</td>
</tr>
<tr>
<td></td>
<td>T–</td>
<td>T – C+</td>
<td>23.8 ± 1.12</td>
</tr>
<tr>
<td></td>
<td>T–C</td>
<td>T – C–</td>
<td>23.5 ± 1.09</td>
</tr>
<tr>
<td>CO2 concentration (ppmv)</td>
<td>C+</td>
<td>T + C+</td>
<td>692 ± 36</td>
</tr>
<tr>
<td></td>
<td>C+C</td>
<td>T + C–</td>
<td>570 ± 54</td>
</tr>
<tr>
<td></td>
<td>C–</td>
<td>T + C–</td>
<td>384 ± 9</td>
</tr>
<tr>
<td></td>
<td>T–C</td>
<td>T – C–</td>
<td>360 ± 8</td>
</tr>
</tbody>
</table>
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 = ±0.06), 9.16 days (±0.10) 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+).](image-url)
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 ± SD) of *T. catappa* seedlings in the four treatments: T + C+ (increased temperature and increased 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 × 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.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Height (cm)</th>
<th>Number of leaves</th>
<th>Total biomass (g)</th>
<th>Total above-ground biomass (g)</th>
<th>Root-to-shoot ratio</th>
<th>SLA (m² g⁻¹)</th>
<th>LDMC (mg g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>T + C+</td>
<td>16.0 ± 5.7</td>
<td>2.5 ± 1.3</td>
<td>0.61 ± 0.24</td>
<td>0.49 ± 0.18</td>
<td>0.29 ± 0.06</td>
<td>32.1 ± 0.86</td>
<td>197 ± 99</td>
</tr>
<tr>
<td>T + C−</td>
<td>17.3 ± 3.9</td>
<td>2.8 ± 1.3</td>
<td>0.59 ± 0.27</td>
<td>0.51 ± 0.20</td>
<td>0.25 ± 0.06</td>
<td>34.7 ± 1.01</td>
<td>203 ± 97</td>
</tr>
<tr>
<td>T − C+</td>
<td>10.4 ± 3.0</td>
<td>1.2 ± 1.2</td>
<td>0.49 ± 0.10</td>
<td>0.39 ± 0.07</td>
<td>0.32 ± 0.05</td>
<td>30.5 ± 1.28</td>
<td>235 ± 187</td>
</tr>
<tr>
<td>T − C−</td>
<td>8.8 ± 3.2</td>
<td>1.0 ± 0.9</td>
<td>0.45 ± 0.16</td>
<td>0.37 ± 0.10</td>
<td>0.32 ± 0.06</td>
<td>27.8 ± 1.47</td>
<td>175 ± 87</td>
</tr>
</tbody>
</table>

**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 somewhat 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.

ACKNOWLEDGEMENTS

We thank Dr. Paulo Horta, Dr. Karla Scherer, Alexandre Schmidt and Lucas Machado for assistance in the installation and maintenance of the experimental setup, and two anonymous reviewers who provided valuable comments on an earlier draft of this manuscript. This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior/Conselho Nacional de Desenvolvimento Científico e Tecnológico (CAPES/CNPq), ‘Science without Borders’ Program through the project ‘Plant interactions and community dynamics in tropical, seasonal systems’ (grant ref. UFSC 114A-2013). HT acknowledges financial support of the University of Potsdam through the Promos scholarship of the Deutscher Akademischer Austauschdienst (DAAD). FIP was recipient of a Pesquisador Visita Especial grant (CAPES/CNPq), and the support is gratefully acknowledged.

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INVASIVE TROPICAL TREE AND CLIMATE CHANGE


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.