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Seasonally Distinctive Growth and Drought Stress Functional Traits Enable *Leucaena Leucocephala* to Successfully Invade a Chinese Tropical Forest

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Abstract

The nitrogen-fixing mimosid *Leucaena leucocephala* continues to be used for afforestation in degraded tropical forests. Yet, fast-growth and high drought stress tolerance enables *L. leucocephala* to outperform native species and *L. leucocephala* has been identified as one of the 100 most invasive species globally. This warrants development of effective control measures, including bio-controls, to prevent the spread of this species particularly across tropical islands. Here, we compare differences in key functional traits between L. leucocephala and eight dominant native species (*Bridelia tomentosa*, *Radermachera frondosa*, *Lepisanthes rubiginosa*, *Rhaphiolepis indica*, *Pterospermum heterophyllum*, *Fissistigma oldhamii*, *Psychotria rubra* and *Cudrania cochinchinensis*) in *L. leucocephala* invaded tropical forests of Hainan Island, China. Functional traits related to growth (photosynthesis rate, stomatal conductance and transpiration rate) and drought stress tolerance (leaf turgor loss point) were measured in wet and dry seasons to investigate whether these functional traits differed between *L. leucocephala* and the eight dominant native species. Our results demonstrate that *L. leucocephal*a has significantly increased growth rates (at least two-fold) in both wet and dry seasons. Additionally, *L. leucocephala* shows significantly higher drought stress tolerance (lower TLP) in the dry season. These results indicate that *L. leucocephala* would almost certainly outperform the eight dominant native species and might successfully invade Hainan tropical forests. There is an urgent need to identify native species that have similar growth and drought stress tolerance traits to enable the development of effective strategies to control *L. leucocephala* on Hainan Island.

Keywords

drought stress tolerance, fast-growing, functional traits, invasion, tropical forest

The fast-growing, nitrogen-fixing species, *Leucaena leucocephala* is widely used for restoring highly degraded tropical forests (Liu et al., 2018; Peng et al., 2019; Wolfe & van Bloem, 2012). Due to its deep roots, capacity to fix nitrogen, drought tolerance capacity, high protein content, and fast foliage growth, it has several potential usages such as serving as livestock fodder, and in controlling soil erosion (Liu et al., 2018; Wolfe & van Bloem, 2012). But it has also become an aggressive invader in many tropical and sub-tropical locations (e.g. on Hawaii islands) and is listed in '100 of the world's worst invasive alien species' (Global Invasive

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Species Database, 2020; Richardson & Rejmánek, 2011). This warrants developing effective control measures (including bio-controls) to prevent the spread of this species, particularly across tropical islands.

Determining the key characteristics/traits of invasive exotic plant species that help them successfully invade the native plant ecosystem is critical their biological control (Funk et al., 2008; Moran et al., 2005; Seastedt, 2015). Traits that help exotic plant species to better adapt to the local environment and are functionally distinct from the native dominant plant species can facilitate invasion (Funk et al., 2008). Moreover, functionally similar plant species cannot coexist (MacArthur & Levins, 1967), and thus mixing plant species that are functionally similar to *L. leucocephala* may help in bio-control of *L. leucocephala*. Indeed, Liu et al. (2018) has found that *Eucalyptus citriodora*, which is functionally similar to *L. leucocephala*, was able to restrict latter's growth.

We hypothesize that *L. leucocephala*'s nitrogen fixation and high drought stress tolerance capacity would, on one hand, help *L. leucocephala* to better adapt to the local environment as compared to the native dominant plant species (e.g., due to its higher growth rate). On the other hand, fast growth and high drought stress tolerance could enable *L. leucocephala* to be functionally distinct from the native dominant species. Thus, fast growth and high drought stress tolerance might be the key characteristics that help *L. leucocephala* to successfully invade tropical forests. To test this hypothesis in a tropical monsoon forest, which has been successfully invaded by *L. leucocephala* in Sanya City (China), we tested whether, i) *L. leucocephala* has significantly higher growth rates across seasons as compared to the native dominant plant species, which have a suppressed growth between wet to dry season; ii) *L. leucocephala* is more drought tolerant than the dominant plant species in dry as well as in wet seasons; and, iii) whether the such high growth rates and drought stress tolerance enable *L. leucocephala* to be functionally distinct from dominant native species in both dry and wet seasons.

Methods

Study Area

The study site is located in Baopoling Mountain (109°30′30″E, 18°19′10″N), at an elevation of 200 m, in Sanya City of the Hainan island, China (Figure 1). The study site has a tropical monsoon oceanic climate with a mean annual temperature of 28°C, precipitation of 1500 mm, with approximately 91% of the precipitation occurring between June to October (Luo et al., 2018). The vegetation of this area is described as tropical monsoon broad-leaf forest. In year 2016, *L. leucocephala* was introduced to recover a 0.2 km^2 highly degraded area in Baopoling Mountain (Figure S1), but within 2 years, the old-growth tropical monsoon board-leaf forest had been successfully invaded by *L. leucocephala* (Figure S1).

Trait Collection and Measurement

We measured functional traits related to plant growth [maximum photosynthesis rate (μmol m^{-2} s^{-1}), stomatal conductance (mmol m^{-2} s^{-1}), and transpiration rate (μmol m^{-2} s^{-1})] and drought stress tolerance

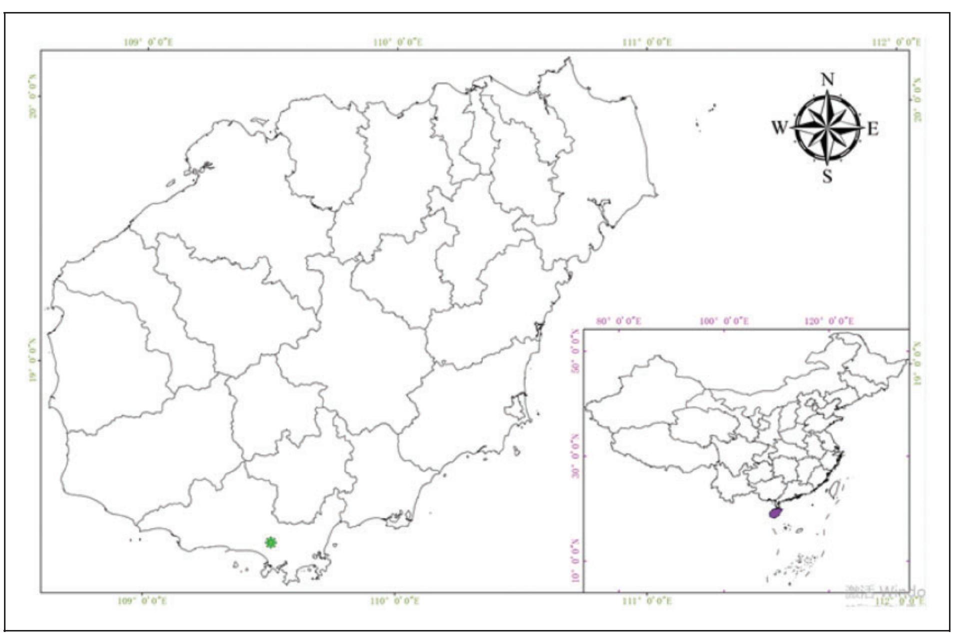

Figure 1. The Map of the Location of the Study Site.

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(leaf turgor loss point, Mpa). All the sampling and measurements were made twice, in the peak of wet (August) and dry seasons (February) in 2019. 30 fully expanded and healthy leaves were collected from five mature individuals of *L. leucocephala* and eight native dominant species (*Bridelia tomentosa, Radermachera frondosa, Lepisanthes rubiginosa, Rhaphiolepis indica, Pterospermum heterophyllum, Fissistigma oldhamii, Psychotria rubra* and *Cudrania cochinchinensis*). We selected individuals that were healthy and with diameters at breast height (DBH) comparable to the mean DBH values of that species (Table S1). Traits were measured following the methods described in Hua et al. (2017) and). Detailed procedures for measuring these functional traits are described in the Supplementary Material.

Data Analysis

We used paired t-test to compare the differences in all the traits between *L. leucocephala* and the eight dominant native species in both the seasons. We used Bartlett's test to insure that all the data met the requirements of homogeneity of variance, as required by paired t-test ($P > 0.05$, Tables S2 and S3). Principal component analysis (PCA) is effective for determining functional traits that could best discriminate plant species (Zhu et al., 2013). Thus, we also utilized PCA to investigate whether the differences in growth rate and drought stress tolerance can (functionally) distinguish *L. leucocephala* from the eight dominant native species.

Results

Our paired t-test results demonstrated that there was no significant variation in *L. leucocephala*'s growth traits (transpiration rate, maximum photosynthesis rate and stomatal conductance) between the two seasons ($P > 0.05$, Figure 2 and Table S4). Whereas, the leaf turgor loss point in the wet season was significantly lower (1/6th) than that in the dry season ($P < 0.05$, Figure 2 and Table S4). In contrast, the eight native dominant species had significantly lower (1/4th–1/2th) transpiration rate, maximum photosynthesis rate, stomatal conductance and leaf turgor loss point in the dry season compared to those in the wet season ($P < 0.05$, Figure 2 and Table S4). Transpiration rate, maximum photosynthesis rate, stomatal conductance and leaf turgor loss point for *L. leucocephala* were 5–10 times higher than all the eight dominant native species in both the seasons ($P < 0.05$, Figure 3 and Table S5). However, there was no difference in leaf turgor loss

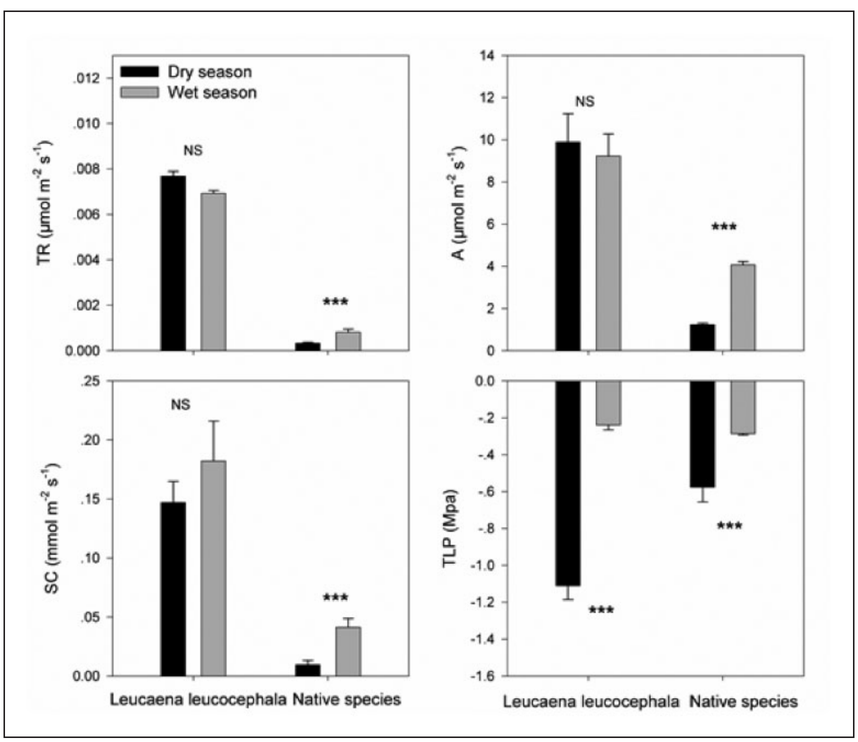

Figure 2. Differences in Functional Traits Associated With a Fast-Growth Strategy (Transpiration Rate (TR, μmol m^{-2} s^{-1}), Maximum Photosynthesis Rate (A, μmol m^{-2} s^{-1}), Stomatal Conductance (SC, mmol m^{-2} s^{-1}) and Leaf Turgor Loss Point (TLP, Mpa)) in Wet and Dry Seasons for the Invasive Exotic Plant Species (*Leucaena leucocephala*) and the Eight Dominant Native Species (*Bridelia tomentosa*, *Radermachera frondosa*, *Lepisanthes rubiginosa*, *Rhaphiolepis indica*, *Pterospermum heterophyllum*, *Fissistigma oldhamii*, *Psychotria rubra* and *Cudrania cochinchinensis*) Respectively. ***indicates $P < 0.001$ and NS (non-significant differences) indicates $P > 0.05$ based on paired t-test.

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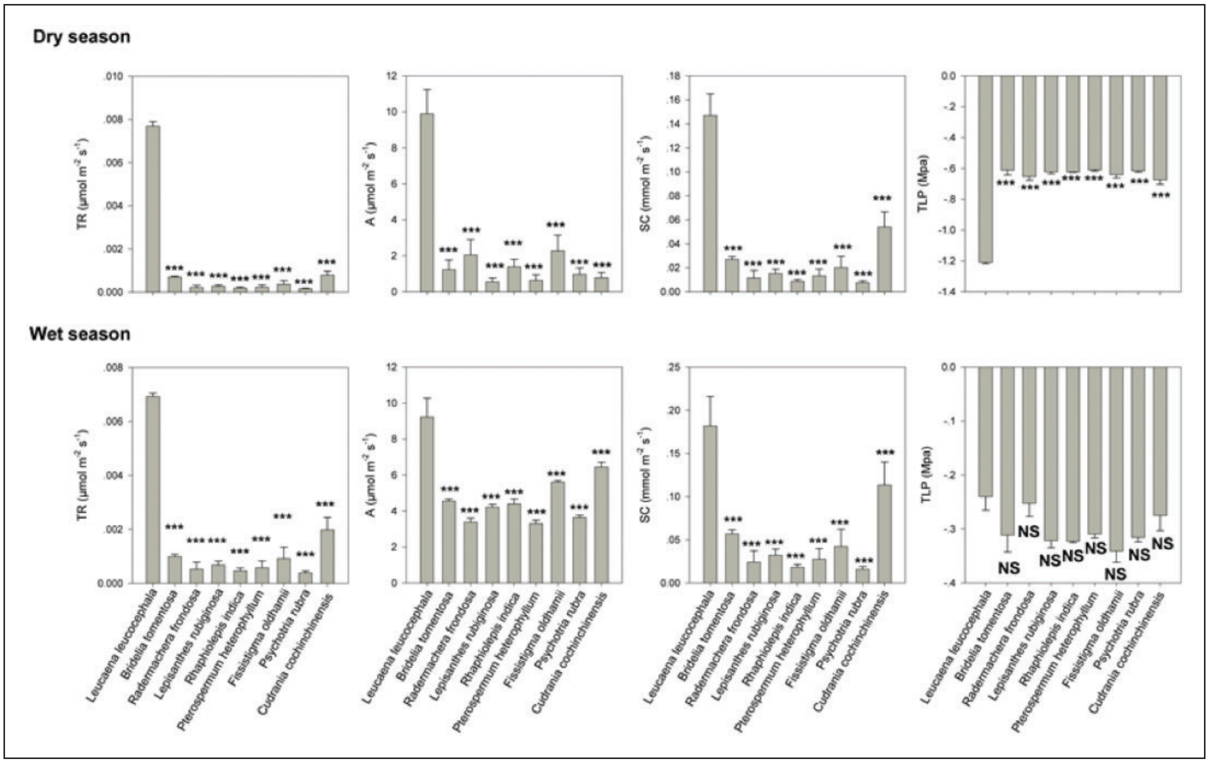

Figure 3. The Differences in the Four Functional Traits (Transpiration Rate, TR; Maximum Photosynthesis Rate, Amass; Stomatal Conductance, SC; and Leaf Turgor Loss Point, TLP) Between the Invasive Exotic Plant Species (*Leucaena leucocephala*) and Each of the Eight Dominant Native Plant Species. *** indicates $P < 0.001$ and NS (non-significant differences) indicates $P > 0.05$ based on paired t-test.

point between *L. leucocephala* and each of the eight dominant species in the wet season. But in the dry season, leaf turgor loss point of *L. leucocephala* was significantly lower (half) than those of the eight dominant species ($P < 0.05$, Figure 3 and Table S5). Results from the PCA showed that all the traits were able to discriminate *L. leucocephala* from the eight dominant native species (Figure 4 and Table 1).

Discussion

Here, we provide evidence to support the hypothesis that higher drought tolerance of *L. leucocephala* in dry season assists in its fast growth throughout the year, as compared to the native dominate species in Hainan forest. Moreover, its high growth rate and drought stress tolerance could functionally distinguish *L. leucocephala* from the dominant native plant species. Thus, our study provides a physiological framework that explains the invasive behavior of *L. leucocephala* in Hainan island.

High photosynthetic rates can result in increased stomatal conductance (Lawson & Vialet-Chabrand, 2019; McAusland et al., 2016) and transpiration rates (Bucci et al., 2019; Maherali et al., 2008; Santos et al., 2018). *L. leucocephala* has evolved leaf traits for maximizing photosynthetic capacity and increasing overall growth, which plausibly facilitates it to outperform the native dominant plant species. Since precipitation in the dry season in this tropical forest is only 1/10th of that in the wet season (Luo et al., 2018), plants are expected to suppress their photosynthesis as the water availability is a key constraint (Guan et al., 2015). Interestingly, photosynthesis rates of *L. leucocephala* were similar in wet and dry seasons, whereas the eight dominant native species suppressed their photosynthesis in the dry season. Therefore, we infer that photosynthesis rate is a key facilitator of *L. leucocephala* in outperforming native species.

No differences in leaf turgor loss point were noticed between *L. leucocephala* and the eight dominant native tree species in the wet season. Leaf turgor loss point is an indicator of water supply (Bartlett et al., 2012). Nearly 90% of the precipitation occurs in the wet season that insures sufficient water supply in this season. Leaf turgor loss point of *L. leucocephala* in the dry season was half of those for each of the eight dominant native species. Under limited water supply, plants with low leaf turgor loss point can maintain high stomatal conductance, photosynthesis and transpiration (Blackman et al., 2010; Mitchell et al., 2008; Sack et al., 2003).

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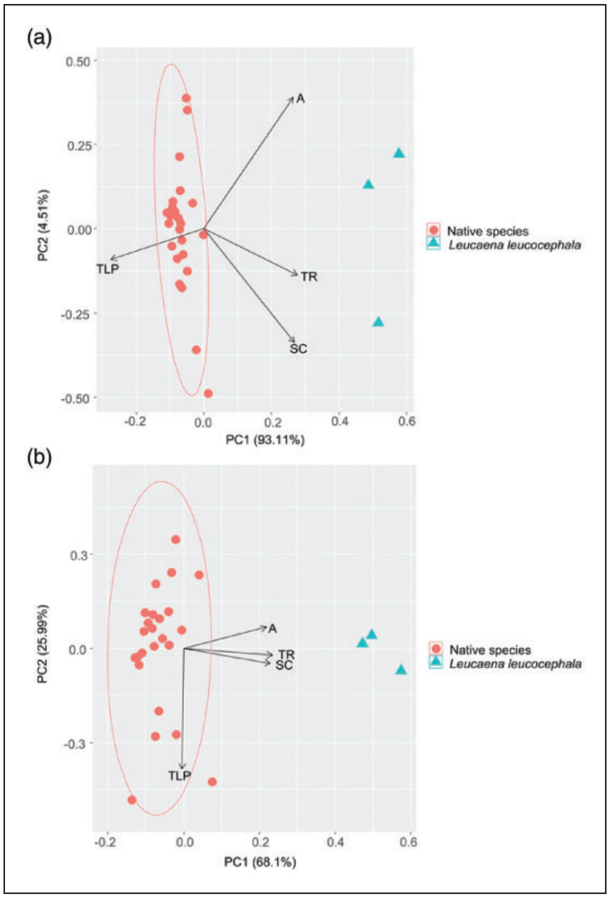

Figure 4. Principal Component Analysis (PCA) of the Four Functional Traits Associated With Fast Growth and Drought Stress Tolerance Between the Invasive Exotic Plant Species (*Leucaena leucocephala*) and the Eight Dominant Native Plant Species.

Table 1. The first two axes of a principal component analysis (PCA) for invasive exotic plant species (*Leucaena leucocephala*) and the eight dominant native species (*Bridelia tomentosa*, *Radermachera frondosa*, *Lepisanthes rubiginosa*, *Rhaphiolepis indica*, *Pterospermum heterophyllum*, *Fissistigma oldhamii*, *Psychotria rubra* and *Cudrania cochinchinensis*), based on four plant functional traits.

Functional traits	PC1	PC2
Transpiration rate	**0.51**	−0.16
Maximum photosynthesis rate	**0.77**	−0.15
Stomatal conductance	**0.58**	−0.19
Leaf turgor loss point	0.11	**0.53**

These include transpiration rate (μmol m^{-2} s^{-1}), maximum photosynthesis rate (μmol m^{-2} s^{-1}), stomatal conductance (mmol m^{-2} s^{-1}) and leaf turgor loss point (Mpa). Bolds indiates significant (PC1 value OR PC2 value >0.5).

Thus, the high drought stress tolerance is critical for *L. leucocephala*'s growth, and assists it in outperforming native species.

The above inferences were supported by the results of PCA analysis, which discriminated *L. leucocephala* from the native species on the basis of four growth- and draught tolerance- related traits (maximum photosynthesis rate, stomatal conductance, transpiration rate and leaf turgor loss point). As the key characteristics of invasive exotic plant species can significantly discriminate them from native plant species (Funk et al., 2008; Laughlin, 2014), we infer that these four traits could enable *L. leucocephala* to be functionally distinct from the native species.

We conclude that fast growth and high drought stress tolerance in the dry season could promote invasion of *L. leucocephala* in the tropical forests. A limitation of our study is that the inferences are drawn from a single year's data. However, previous studies have also found that high growth rate and drought stress tolerance can help *L. leucocephala* to successfully outperform the native forest species (Barros et al., 2020; Chiou et al., 2016; Wolfe & van Bloem, 2012). Therefore, it is safe to conclude that fast-growing capacities in wet as well as in dry seasons, and high drought stress tolerance in the dry season are the key traits that help *L. leucocephala* to successfully invade tropical forests.

Implications for Conservation

The results of this study clearly revealed that *L. leucocephala* outperforms the eight dominant native species and can successfully invade Hainan tropical forests. There is an urgent need to identify native species that have similar growth and drought stress tolerance traits to enable their development as part of an effective strategy to control *L. leucocephala* invasion of forests on Hainan Island. Here, we have demonstrated that four functional traits (maximum photosynthesis rate, stomatal conductance, transpiration rate and leaf turgor loss point) can facilitate *L. leucocephala* to successfully invade the tropical forest. These four traits can be utilized to develop a 'native species selection' software (details see Wang et al., 2020) that would assist in the selection and deployment of multiple native tree species that are functionally similar to *L. leucocephala* for bio-control of *L. leucocephala* on Hainan island.

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Declaration of Conflicting Interests

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Supplemental material

Supplemental material for this article is available online.

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