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Influence of Drought and Shade on Seedling Growth of Native and Invasive Trees in the Seychelles

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ABSTRACT

We studied the growth of seedlings of native and invasive tree species from secondary tropical forests on Mahé (Seychelles). We were interested in whether native or invasive species are more drought-tolerant, and therefore conducted a garden (pot) experiment comparing the growth of seedlings of five native and five invasive tree species under different light (7% and 60% transmittance) and water (natural and repeated drought stress) conditions. Differences in the responses of native and invasive species to these treatments were small. In both groups, mean relative growth rates were reduced only slightly by intermittent drought that caused wilting of leaves. However, invasive species produced clearly thinner leaves (high specific leaf area, SLA) and more root biomass than native species under high light, while these differences were small under low light. Native species performed better than invasive species under low light with low water availability. It appears that high phenotypic plasticity allows some fast-growing invasive species to cope with water stress by adjusting the relative allocation of resources to aboveground and belowground structures under high light, while this strategy is not effective when both light and water resources are limiting. We conclude that water stress may reduce the invasibility of shaded habitats by fast-growing invasive species, while water stress in unshaded habitats may have less effect on invasive species than previously recognized.

Key words: biomass allocation; drought stress; invasiveness; light availability; oceanic islands; RGR; tropical tree seedlings.

WHY SOME HABITATS ARE LESS INVADED THAN OTHERS IS A CENTRAL QUESTION IN INVASION BIOLOGY to which there are still no fully satisfying answers. The relative importance of biotic factors is still debated (Levine *et al.* 2004), but there is general agreement that many invasive species benefit from high levels of abiotic resources, particularly light and nutrients (Davis *et al.* 2000, Lake & Leishman 2004, Maskell *et al.* 2006, Schumacher 2007). For instance, it has been shown that nutrient enrichment strongly promotes the spread of alien species in low fertility shrubland in southeastern Australia (Lake & Leishman 2004), while increased light availability due to anthropogenic disturbance is an important factor enabling plant invasions into tropical forests (Fine 2002). Based on such empirical results, it has been proposed that pulses of resources exceeding the immediate needs of the established community increase the vulnerability of habitats to invasion (Davis *et al.* 2000), while very low levels of resources make habitats resistant to invasion (Alpert *et al.* 2000). A few studies suggest that low soil-water availability reduces the invasibility of a habitat (Alpert *et al.* 2000, Stohlgren *et al.* 2001). For example, in growth experiments comparing the performance of native and invasive species under varying environmental conditions, Daehler (2003) found that native species in Hawaii suffered less from water stress than invasive species. There is also evidence that increased availability of water may facilitate plant invasions into drier habitats (Milchunas & Lauenroth 1995).

Subtle gradients in water availability are known to have a considerable effect upon the distribution of tree species in tropical forests (Bongers *et al.* 1999, Engelbrecht *et al.* 2007). Although the seedlings of some light-demanding pioneer trees are sensitive to drought, and may be killed by even short dry spells (Engelbrecht *et al.* 2006), seedlings of shade-tolerant species may be more vulnerable because of their low growth rates and thin leaves (Veenendaal *et al.* 1996, Turner 2001). Shifts in the frequency of dry periods due to climate change could therefore influence the species composition of tropical forests considerably (Condit 1998, Whitmore 1998), partly by altering their resistance to alien species.

We examined the influence of soil-water availability on plant invasions in tropical forests on the mountainous island of Mahé (Republic of Seychelles, Indian Ocean). These forests had a number of advantages for our purposes. First, the isolated flora of the Seychelles has experienced a long history of climatic changes (Stoddart 1984, Briggs 2003) and the native species are presumably adapted to a broad range of conditions from dry to very humid (Stoddart 1984, Schumacher *et al.* 2003). Secondly, Mahé contains a diversity of habitats ranging from relatively dry, sun-exposed inselbergs (sparse shrub vegetation on granite outcrops) to montane mist forests, all of which have been invaded to some degree by alien woody plants. Thirdly, despite its high environmental heterogeneity, there are only approximately 20 abundant woody species on the Seychelles, with less than half of them being invasive species. This makes it possible to compare the growth characteristics of invasive and native woody species along extensive gradients of water and light availability.

In this study, we test the hypothesis that native woody plant species of the granitic islands of the Seychelles are better able to cope with drought than invasive plant species. In a garden (pot) experiment, we compared the growth of seedlings of five native and five invasive species under two light intensities representing forest gap and shade conditions and two water levels (continuously moist and intermittent drought).

METHODS

GENERAL STUDY AREA.—The study was carried out on Mahé, the main inner island of the Republic of Seychelles (4° S, 55° E, total area 154 km^2, 0–900 m asl). Like the other inner islands of the

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Seychelles, Mahé is composed of granitic rock 550- to 650-million-years old that has never been submerged (Stoddart 1984). As a result, the soils are mostly highly weathered ferrasols with a pH of *ca* 4.5 and nutrient poor (Kueffer 2006).

The forest vegetation of Mahé was heavily affected by human activities until the 1970s, and is mostly secondary and dominated by alien trees, especially *Cinnamomum verum* (Kueffer *et al.* 2007). In contrast, the sparser vegetation on nutrient poor, sun-exposed granitic rock outcrops (inselbergs) is much less invaded, with >80 percent cover by indigenous plant species (Fleischmann *et al.* 1996, Fleischmann 1997).

The inland habitats at low-to-intermediate altitudes (<650 m asl) have a humid tropical climate with a mean annual rainfall of 1600–3300 mm depending on altitude (Stoddart 1984, Cazes-Duvat & Robert 2001, Kueffer *et al.* 2007). Although there is no pronounced seasonality in rainfall, the period from June through September is generally drier (mean monthly rainfall: 80–150 mm) than from November through February (300–450 mm) (Cazes-Duvat & Robert 2001). During the wet period there are usually *ca* 10 d per month with < 0.1 mm rainfall per day, while during the dry period there are about 15 dry days per month (based on data for the past 30 yr from Meteo Seychelles). Monthly mean temperatures are 26–28°C at sea level and approximately 2°C lower in the understory of intermediate altitude forests (Kueffer 2006; Meteo Seychelles). During their long history, the granitic islands of the Seychelles have experienced many changes in climate (Stoddart 1984, Briggs 2003), *i.e.*, because rain is mainly orographic precipitation was strongly influenced by shifts in wind patterns and by sea-level changes during the Quaternary period (Stoddart 1984).

Species.—We selected five invasive and five native broad-leaved, evergreen tree species that are abundant in low-to-intermediate altitude secondary forests and inselberg vegetation in the Seychelles and for which seeds were available at the time of the experiment (Table 1). The native species included three endemic species. Most of the invasive species were introduced to the islands in the late 19th or early 20th centuries, but *C. verum* and *Syzygium jambos* were introduced > 200 yr ago (Kueffer & Vos 2004). The seeds of all species are similar in size (2–10 mm diameter) except for *S. jambos,* which has larger seeds (15–20 mm diameter). Nomenclature follows Friedmann (1994).

Common garden experiment.—The experiment was conducted on a level, unshaded site at the Sans Souci forestry station on the east slope of Morne Seychellois (4°38′ S, 55°27′ E; 380 m asl). Seedlings of *S. jambos, Tabebuia pallida, Memecylon eleagni*, and *Paragenipa wrightii* were grown from seed collected in the forests of Mahé. Ripe fruits were collected either directly from 5 to 15 parent trees or from the ground beneath them (*S. jambos*). Immediately after collection, the seeds were cleaned and sown into trays. When the seedlings had developed their primary leaves (3–6 mo after sowing) they were transplanted into 1-L pots. Because the seeds obtained for the remaining species (*Alstonia macrophylla, C. verum, Psidium cattleianum, Aphloia theiformis, Canthium bibracteatum*, and *Erythroxylum sechellarum*) were insufficient, we collected seedlings of similar size to those grown from seed and planted them directly into pots. The soil in the pots was a mixture of organic forest topsoil and laterite subsoil (35% organic soil, 65% laterite soil, by volume), and was relatively infertile compared to most tropical soils (Kjeldahl N 1.7 mg/g; P 0.28 mg/g). Before the start of the experiment, all seedlings were allowed to adjust to the pot environment for at least two weeks.

TABLE 1. *Characterization of the study species used in the common garden experiment. The experiment started on 27 May 2003 (duration 117–121 d). The soil water content below which a particular species was watered in the drought stress treatment is also indicated. See text for further information. Nomenclature and maximal stem height after Friedmann (1994).*

Species	Family	Maximal stem height (m)	Soil water content at wilting point (vol %)
Invasives			
Alstonia macrophylla Wall. Ex G. Don	Apocynaceae	15	13
Cinnamomum verum Presl	Lauraceae	15	9
Psidium cattleianum Sabine	Myrtaceae	7	6
Syzygium jambos (L.) Alston	Myrtaceae	10	10
Tabebuia pallida (Lindl.) Miers	Bigogniaceae	10	9
Natives			
Aphloia theiformis^{+} (Vahl) Benn	Flacourtiaceae	12	11
Canthium bibracteatum (Baker) Hiern	Rubiaceae	8	13
Erythroxylum sechellarum* O.E. Schulz	Erythroxylaceae	7	9
Memecylon eleagni* Bl.	Melastomataceae	10	8
Paragenipa wrightii* (Baker) F. Friedmann	Rubiaceae	6	8

$^{+}$subsp. *madagascariensis* (Clos) H. Perr. var. *seychellensis* (Clos).

*species endemic to the Seychelles.

Two light levels were used to represent conditions in the forest understorey (low radiation, LR; 7% of ambient light) and in gaps (high radiation, HR; 60% of ambient light) of relatively open secondary forests in Seychelles (Kueffer *et al.* 2007). These light conditions were achieved by using green shade-cloth with appropriate light transmittance (Agroflor, Austria). The shade-cloth was covered with clear polyethylene foil (0.1-mm thickness and 15% absorbance) as protection from rain. Light levels were calibrated using a photosynthetically active radiation (PAR) quantum sensor. Temperature beneath the shade-cloth tended to be somewhat higher (36°C vs. 32°C) and relative humidity was lower (60% vs. 75%) under HR compared to LR (measurements were made at noon on sunny days and thus represent maximum differences).

The two water treatments were intended to represent continuously moist conditions (W; pots watered every other day) and intermittent drought (D; pots watered when soil reached the species-specific wilting point of soil water content). In a preliminary study, the soil water content at wilting point was separately determined for each species using a tensiometer (Model HH2 with a Theta Probe type ML2x, delta-T Devices, England).

A split-plot design was used with light as the main factor and water treatment as the split-plot factor. For each species seven plants per treatment were randomly assigned to the four treatment combinations. At monthly intervals, the plants were redistributed among the six shade-cloth 'greenhouses' by light treatment. There was at least one replicate per species and water treatment under each greenhouse at any one time. The experiment was started on 27 May 2003 and was terminated after 117–121 d.

DATA COLLECTION.—At the start of the experiment, four randomly chosen seedlings of each species were harvested to determine initial total dry weight. From the remaining seedlings the following parameters were recorded at 8-week intervals: stem height; number of leaves; length and breadth of all leaves; and basal stem diameter. As the basis for estimating leaf area of the experimental plants, linear regressions of leaf area on the product of leaf length and width were calculated for a sample of > 100 leaves per species from seedlings collected in the field. The sample leaves were placed beneath a glass plate and photographed with a digital camera (Nikon Coolpix 995, resolution at 2048 × 1536 pixels). These images were used to determine leaf length and width using Adobe Illustrator^{TM} 10, and leaf area using Adobe Photoshop^{TM} 7.0 (Dietz & Steinlein 1996). At the end of the experiment, all live plants were harvested and separated into three fractions; leaves, stems plus petioles, and roots, and these were oven-dried at 80°C for 48 h.

The raw data were used to calculate the following growth parameters:

$\mathbf{RGR_{DW}}$ (Relative growth rate by dry weight)

$$= \frac{\ln(\text{dry weight at end}) - \ln(\text{dry weight at start})}{\text{duration of experiment}}$$

$\mathbf{RGR_{LA}}$ (Relative growth rate by leaf area)

$$= \frac{\ln(\text{leaf area at end}) - \ln\,(\text{leaf area at start})}{\text{duration of experiment}}$$

$$\textbf{SLA}\ (\text{Specific leaf area}) = \frac{\text{leaf area}}{\text{dry leaf biomass}}$$

$$\textbf{LAR}\ (\text{Leaf area ratio}) = \frac{\text{leaf area}}{\text{dry plant biomass}}$$

$$\textbf{RSR}\ (\text{Root : shoot ratio}) = \frac{\text{dry root biomass}}{\text{dry shoot biomass}}$$

STATISTICAL ANALYSIS.—We used general linear models with light level, water level, species status (native or invasive), and the corresponding factor interactions as fixed factors; and species identity (nested in species status) as a random factor. The leaf area of each plant at the start of the experiment was included as a covariable to account for differences in initial plant size. Dependent variables were plant growth (relative growth rate of total dry weight, and leaf area) and allocation (SLA, LAR, RSR). To ensure homoscedasticity, SLA, LAR, and RSR were log transformed. All statistical analyses were performed with JMP V 6.0 (SAS Institute Inc., 2005).

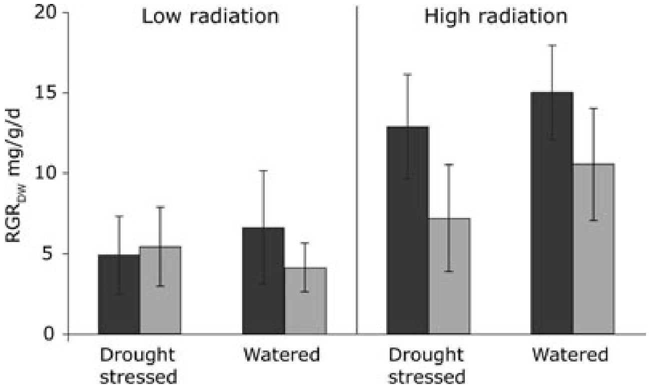

FIGURE 1. Relative growth rate of total dry weight (RGR_{DW}) of invasive (black bars) and native (gray bars) species (mean ± SE) under two light levels and two water treatments (drought stressed vs. watered). See text for further information.

RESULTS

MORTALITY.—For most species, seedling mortality during the experiment was low. Exceptions were *T. pallida* in the LR and drought treatment, and *M. eleagni* in the HR and water treatment (five of seven seedlings died). In 70 percent of the remaining species-treatment combinations all seedlings survived, and in the other cases only one or two individuals died. Mortality was higher among drought-stressed native species, with deaths occurring in 70 percent of these species-treatment combinations, compared to 23 percent among the other combinations.

RELATIVE GROWTH RATE.—There was large variation in relative growth rate of total dry weight (RGR_{DW}) among species within groups. Under LR, values ranged from −0.9 to 12 mg/g/d for both species groups, and under HR 9–24 mg/g/d for invasive plants and 3–20 mg/g/d for native plants. Both native and invasive species grew fastest (RGR_{DW} and relative growth rate of total leaf area RGR_{LA}) under HR ($P < 0.001$; Fig. 1; Table 2), but the response to light tended to be greater among invasive species (species group × light, $P \leq 0.09$). Compared to ambient water conditions (W), drought (D) reduced mean growth rates (both RGR_{DW} and RGR_{LA}) by 4 percent under LR and 28 percent under HR ($P \leq 0.004$; Fig. 1; Tables 2 and 3). This greater reduction in relative growth under HR is reflected in a significant interaction between light and water in the ANOVA ($P < 0.01$; Table 2).

The mean RGR_{DW} of invasive species was 40–80 percent higher than that of native species under all treatments except under

TABLE 2. *Results of ANOVA across two levels of light and watering. Indicated are the* F- *and* P-*values of main effects and interactions for the following parameters (df = 1): relative growth rates of total dry weight (RGR$_{DW}$) and leaf area (RGR$_{LA}$), root dry weight (Root$_{DW}$) specific leaf area (SLA), leaf area ratio (LAR), and root:shoot ratio (RSR). Significant values are indicated in bold.*

	RGR$_{DW}$		RGR$_{LA}$		Root$_{DW}$		SLA		LAR		RSR	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species group^{+} (S)	1.8	0.215	3.4	0.099	17.2	**0.004**	2.2	0.175	1.2	0.310	3.1	0.115
Light (L)	216	**< 0.0001**	24.7	**< 0.0001**	143	**< 0.0001**	244	**< 0.0001**	110	**< 0.0001**	32.4	**< 0.0001**
S × L	3.6	0.095	1.1	0.327	22.5	**0.002**	3.9	0.086	1.8	0.222	2.3	0.174
Water (W)	24.5	**0.004**	26.1	**0.001**	9.6	**0.018**	14.9	**0.031**	7.3	**0.030**	3.6	0.097
S × W	2.3	0.186	1.8	0.226	2.6	0.151	2.1	0.249	0.5	0.494	0.04	0.856
L × W	7.8	**0.006**	7.1	**0.008**	14.1	**0.0002**	0.02	0.885	0.5	0.494	0.1	0.706
S × L × W	7.4	**0.007**	8.1	**0.005**	0.9	0.357	0.3	0.608	0.9	0.341	2.7	0.104
Initial leaf area	17.2	**< 0.0001**	21.8	**< 0.0001**	140	**< 0.0001**	1.1	0.293	5.2	**0.023**	3.2	0.077

$^{+}$native vs. invasive.

LR and drought, but these differences between species groups were not significant (overall species group effect $P = 0.2$; Fig. 1; Table 2). However, while drought reduced the mean growth rate of invasive species by approximately 20 percent irrespective of light availability, it reduced the growth of native species only under HR, and growth rates under LR were actually 40 percent higher in the drought stress treatment than when watered. Thus, there was a significant three-way interaction between water, light, and species group ($P < 0.008$, Fig. 1).

BIOMASS ALLOCATION.—*Specific leaf area and leaf area ratio*. Mean SLA was 75–245 cm^2/g under HR, and 80–550 cm^2/g under LR. Overall, SLA did not differ significantly between the two species groups ($P = 0.2$), though mean values of SLA were about 60 percent higher in invasive than in native plants under HR, and 20 percent higher under LR. Thus, in the invasive plants, phenotypic plasticity of SLA was greater in response to light, though the interaction was not significant (species group × light interaction; $P = 0.09$). Under HR, SLA was 45 percent lower in the invasive and 25 percent lower in the native species than in the respective LR treatments ($P < 0.001$; Tables 2 and 3). In the drought treatment, SLA was also reduced compared to the watered controls, by 10 percent in the invasive plants and by 5 percent in the native plants ($P < 0.05$). Again, there were no significant differences between species groups. The leaf area ratio (LAR) was positively correlated with SLA ($r > 0.4$, $P < 0.001$; Tables 2 and 3) and responded similarly to the various treatments; the results are therefore not presented in detail.

Root dry weight and root:shoot ratio. Under LR, most seedlings showed only a small increase in root dry weight during the experiment (Fig. 2). However, roots grew larger under HR, especially in the invasive species, so that seedlings of the invasive species achieved a much higher root dry weight than native species (species group × light, $P = 0.002$; Fig. 2; Table 2). In both species groups, root:shoot ratio (RSR) was significantly higher under higher radiation ($P < 0.001$), but there were no clear effects of the water treatment ($P = 0.1$; Table 2). RSR of the native species tended to be lower than that of invasive species ($P = 0.1$; Table 2).

DISCUSSION

The water-stress treatment applied in our experiment was severe, *i.e.*, the tree seedlings were exposed to periodic dry spells sufficient to induce leaf wilting, and the relatively high air temperature and low

Table 3. *Means (± SE) of response variables per species group (native vs. invasive). See Table 2 for acronyms.*

		Low radiation		High radiation	
		Drought stressed	Watered	Drought stressed	Watered
RGR$_{LA}$	*invasive*	0.006 (0.002)	0.008 (0.005)	0.009 (0.003)	0.012 (0.003)
(cm^2/cm^2/d)	*native*	0.005 (0.002)	0.003 (0.002)	0.003 (0.003)	0.008 (0.003)
SLA	*invasive*	272 (63)	309 (80)	148 (19)	166 (26)
(cm^2/g)	*native*	168 (25)	174 (28)	126 (16)	133 (15)
LAR	*invasive*	96 (21)	117 (42)	53 (8)	61 (10)
(cm^2/g)	*native*	73 (11)	78 (15)	49 (6)	56 (10)
RSR	*invasive*	0.52 (0.06)	0.46 (0.06)	0.65 (0.05)	0.61 (0.02)
	native	0.40 (0.05)	0.39 (0.03)	0.49 (0.07)	0.45 (0.05)

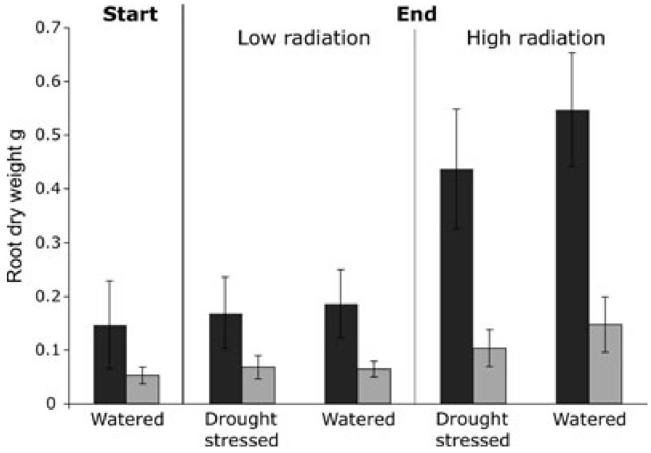

FIGURE 2. Root dry weight (Root$_{\mathrm{DW}}$) of invasive (black bars) and native (gray bars) species (mean ± SE) at the start and end of the experiment.

relative humidity in the experimental tents may have increased the severity of the drought treatment. Nevertheless, average growth rates decreased by only 10–20 percent, and the morphological responses to drought, although small, were as expected from other studies—including thicker leaves, lower leaf area (LAR), and higher RSR (Burslem *et al.* 1996, Baruch *et al.* 2000, Poorter & Hayashida-Oliver 2000). The weak but consistent response to the water-stress treatment indicated that most species were able to recover from short episodes of drought. We drought-stressed the experimental plants to the same soil-water level throughout the experiment, and therefore severity of the water-stress treatment may have changed with the duration of the experiment. However, we did not observe any obvious variation in mortality patterns or the occurrence of leaf wilting at the end of drought cycles with increased duration of the experiment.

DIFFERENCES BETWEEN NATIVE AND INVASIVE SEEDLINGS IN THEIR RESPONSE TO RESOURCE SHORTAGE.—While there was considerable variation in growth responses to the light and water treatments within both groups of species, the differences between native and invasive species were mostly small. In particular, contrary to our expectation, growth rates of invasive species were on average not more affected by water stress than native species. It could be argued that the generally lower mortality of invasive species in the drought treatment was because the plants produced more roots than native species (Fig. 2). However, in our experimental design we reduced soil moisture content separately for each species to a value where the particular species showed signs of wilting. In this way, we excluded the possibility that plants avoided water shortage by producing a larger root mass.

The large variation within groups and the relatively small differences between groups, corroborate Schumacher's hypothesis (2007), based on responses of native and alien juveniles to increased light and nutrient availabilities, that the dichotomy between plastic and fast-growing species and stress-tolerant species is not a general distinction between native and invasive species, and that both strategies occur to some extent within both species groups. In fact, the range of soil moisture contents at leaf wilting was similar in both species groups (Table 1), and the species with the lowest wilting point (6% soil moisture) was the invasive *P. cattleianum*, which also proved to be very shade-tolerant (Schumacher 2007). This helps to explain why this species is highly invasive in both shady, montane mist forests and on the very exposed, dry inselbergs (Fleischmann 1997, Kueffer & Vos 2004).

The fast-growing invaders, *A. macrophylla* and *T. pallida*, were strongly affected by the drought treatment. However, this was mainly in low light conditions, in which drought stress treatment reduced RGR of *A. macrophylla* by 30 percent compared to ambient water conditions, and five of seven *T. pallida* individuals died. In contrast, growth rates of the fast-growing native species, *A. theiformis* and *C. bibracteatum,* were higher under drought stress and low light. These results indicate that the fast-growing invasive species were particularly sensitive to a combination of drought and low light; we suggest that this sensitivity reflects their strategies for coping with these stresses. Even if invasive species have a lower physiological ability to tolerate resource shortage, as predicted by our hypothesis, they may compensate for this to some degree through higher morphological plasticity. This allows them to increase allocation to the organs responsible for the uptake of whatever resource is limiting, *i.e.*, a high specific leaf area (SLA) under low light and a high RSR in drought conditions. As a result, when there are deficiencies of both light and water, morphological plasticity is not an effective strategy because the optimal allocation patterns conflict with each other (Veenendaal *et al.* 1996, Niinemets & Valladares 2006). Other studies have also shown phenotypic plasticity to be an important mechanism allowing invasive species to cope with low resource conditions (Richards *et al.* 2006, Schumacher 2007). For instance, an invasive species proved to be more plastic than native species in response to drought stress in a dry subtropical forest (*Schinus terebinthifolius*; Stratton & Goldstein 2001) and in an alpine ecosystem (*Taraxacum* sp.; Brock & Galen 2005). In contrast, many native trees in Seychelles show little phenotypic plasticity in response to differing light and nutrient conditions (Schumacher 2007). We conclude that high phenotypic plasticity allows fast-growing invasive species in Seychelles to compete successfully with more stress-tolerant species in sites where resources are in moderately short supply. However, this strategy does not enable them to grow under conditions where both light and soil resources are strongly limiting.

IMPLICATIONS FOR TREE REGENERATION IN THE SEYCHELLES.—Water shortage is unlikely to be an important factor limiting tree regeneration in the tropical forests of the Seychelles. The mortality of plants in the pot experiments was mostly low even in the drought treatment, where soil moisture contents were repeatedly reduced to 6–12 percent. In the sandy loam laterite soils used in the experiment (*ca* 70% sand, 15% silt, 15% clay; Schumacher unpubl. data), these water contents correspond to water potentials of well below −1.5 MPa (derived from soil-moisture characteristic curves of laterite and organic soils collected in secondary forests in Seychelles; Sedivy Mylonas & Kueffer unpubl. data), which is cited as the permanent wilting point of many plants (Lambers *et al.* 1998). Furthermore, the average intervals between watering in the drought treatment (10 d in high light and 15 d in low light) were also longer than typical dry spells on Mahé. According to weather records at sea level, in the past 30 yr there have been only 18 dry periods on Mahé lasting longer than 9 d (*i.e.*, < 0.1 mm/day) and six lasting longer than 14 d (Meteo Seychelles; Mahé airport). However, these more extreme drought events could be more detrimental to slow-growing native species than indicated by our experiment. This is because seedlings of native species initially tend to have smaller roots than those of invasive species, either because their root mass is smaller after germination or because they grow more slowly (Fig. 2), so that it may take longer before young plants are sufficiently established to withstand a severe drought.

In conclusion, our experiment does not support our hypothesis that invasive species generally are less drought-tolerant than native species, and therefore differences in drought-tolerance are unlikely to explain why the driest habitats in the Seychelles, the inselbergs, are also the least invaded (Fleischmann 1997). It appears that high phenotypic plasticity allows some fast-growing invasive species to cope with water stress by adjusting the relative allocation of resources to aboveground and belowground structures under high light, while this strategy is not effective when both light and water resources are limiting. Water stress may therefore reduce the invasibility of shaded habitats by fast-growing invasive species such as *T. pallida*, a species that is notably absent from inland closed-canopy forests in Seychelles (Kueffer & Vos 2004), while in unshaded habitats water stress may have less effect on invasive species than previously recognized.

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