American Journal of Botany

American Journal of Botany 98(2): 1–8. 2011.

DIFFERENTIAL RESPONSES TO GUANO FERTILIZATION AMONG TROPICAL TREE SPECIES WITH VARYING FUNCTIONAL TRAITS

HILLARY S. YOUNG[1,3], DOUGLAS J. MCCAULEY[1,2], AND RODOLFO DIRZO[1]

[1] Department of Biology, Stanford University, 371 Serra Mall, Stanford, California 94305 USA; and [2] Hopkins Marine Station, Stanford University, 100 Oceanview Blvd., Pacific Grove, California 93950 USA

- ***Premise of the study*:** Seabirds often cause significant changes to soil properties, and seabird-dominated systems often host unique plant communities. This study experimentally (1) examined species-specific responses to seabird guano gradients, (2) considered the role that differential functional traits among species play in altering plant response to guano, and (3) investigated the implications of seabird guano on range-expanding species.
- ***Methods*:** Using a greenhouse fertilization experiment, we examined how guano fertilization affects the growth and functional traits of four tree species dominant in the Pacific Islands: *Cocos nucifera, Pisonia grandis, Scaevola sericea,* and *Tournefortia argentea*. In these systems, seabirds are frequently found in association with three of these four species; the remaining species, *C. nucifera*, is a recently proliferating species commonly found in the region but rarely associated with seabirds.
- ***Key results*:** We determined that responses to guano addition differed significantly between species in ways that were consistent with predictions based on differing functional traits among species. Notably, we demonstrated that *C. nucifera* showed no growth responses to guano additions, whereas all seabird-associated plants showed strong responses.
- ***Conclusions*:** These results provide experimental evidence of differential species response to guano additions, suggesting that differences in species functional traits may contribute to changes in plant communities in seabird-dominated areas, with seabird-associated species garnering performance advantages in these high-nutrient environments. Among these species, results also suggest that *C. nucifera* may have a competitive advantage in low-nutrient environments, providing an unusual example of how a range-expanding plant species can profit from low-nutrient environments.

Key words: functional traits; guano inputs; seabirds; tropical forests, *Cocos nucifera, Pisonia grandis, Scaevola sericea, Tournefortia argentea*.

Seabird guano is well established as an important nutrient subsidy for soils, concentrating nutrients from surrounding marine environments into terrestrial nesting or roosting areas (Hutchinson, 1950; Ellis, 2005). Across a wide range of ecosystems, increased abundance of seabirds consistently results in marked increases in soil nitrogen and phosphorus (Mulder et al., in press). Seabird guano also affects levels of micronutrients, soil pH, soil moisture, and soil salinity, though these effects are more variable (García et al., 2002; Ellis, 2005). These guano-driven changes in soil characteristics often lead to substantial changes in multiple aspects of plant communities, including alterations in total plant cover, plant biomass, and plant nutrient status (Ellis, 2005; Maron et al., 2006; Wait et al., 2005). Positive effects on plant growth or foliar nutrients have been generally attributed to increased availability of macronutrients (Anderson and Polis, 1999; Ellis, 2005). Negative effects, usually observed at extremely high bird densities, also have been observed and are usually attributed to ammonium toxicity or low pH, which can inhibit nutrient uptake (Odasz, 1994; Britto and Kronzucker, 2002).

These established effects of seabirds on soil and foliar nutrients suggest predictable changes in plant community composition also may exist along seabird gradients. Analysis of plant communities along seabird gradients shows that indeed increased seabird abundance often leads to pronounced differences in community species composition. Generally, high-bird sites are characterized by plant communities with lower diversity and more invasive species (Sobey and Kenworthy, 1979; Hogg et al., 1989; Kamijo and Yoshinobu, 1995; Ellis et al., in press). Clear patterns of plant taxonomic association also appear to exist with seabird-dominated sites, with increased abundances of Apiaceae, Brassicaceae, Chenopodiaceae, Poaceae, and Solanaceae in high-seabird sites (Vidal et al., 2000; Ellis et al., in press). Vidal et al. (1998) suggested that differences in plant functional traits explain many of these community shifts, and they demonstrated correlations between growth form and seed size and abundance of gulls. However, there has been little work correlating other functional traits (i.e., foliar nutrients, specific leaf area [SLA], chlorophyll, growth rates) with seabird abundance, despite strong theoretical links of these traits to seabird-driven environmental heterogeneity.

Since increased abundance of seabirds should reduce nutrient stress for plants (until such a point at which the subsidies cause toxicity), increased seabird abundance would be likely to favor "competitor" species with functional traits that allow plants to achieve a high rate of resource acquisition over short time periods (Vidal et al., 2000; Grime, 1977, 2001). Functional traits typical of these competitor species include high relative

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[1] Manuscript received 1 May 2010; revision accepted 6 December 2010.

The authors thank the National Science Foundation, the National Geographic Society, the Woods Institute for the Environment, and the Stanford Gabilan Graduate Fellowship for their financial support. For advice throughout this study they thank T. Raab, F. Micheli, and P. Vitousek. Invaluable analytical assistance was provided by D. Turner. For assistance in the nursery and laboratory the authors thank R. von Itter, D. Wilson, A. Briggs, W. Love-Anderegg, J. McCallen, Ana Miller-ter Kuile, V. Walbot, and C. Pinto.

[3] Author for correspondence (e-mail: hsyoung@stanford.edu); phone: 619-889-7520; fax: 650-723-6132

doi:10.3732/ajb.1000159

growth rates (RGR), high photosynthetic rates, high chlorophyll levels, high SLA, high foliar nutrient levels, and short leaf life span, among many other traits (Tilman, 1988; Reich et al., 1997). In contrast, sites with low seabird abundance (that are not otherwise nutrient rich) should favor more "stress tolerant" plant species with low RGR, low chlorophyll levels, high SLA, and lower foliar nutrients. Sites with extremely high seabird abundance, where ammonium may reach toxic levels and/or nutrients may become unavailable because of guano-driven reductions in pH, could preferentially favor either stress-tolerant plants or advantage competitor plants that are adapted to cope with these conditions (Wait et al., 2005). However, extremely high densities of seabirds often also cause extensive physical disturbance to plants in their roosting or nest-building activities; thus, the physical stress characteristic of these situations could further change plant community structure, favoring more resilient ruderal species (Vidal et al., 2003).

In this study we experimentally examined plant performance responses to variable levels of guano addition between seabird-associated plant species and plant species that occur in similar sites without seabirds. These experimental tests are particularly important for understanding how seabird-derived nutrients alter plant communities, as it is often difficult to define the relative importance of nutrient additions as opposed to physical disturbance of seabirds (Vidal et al., 1998, 2000; Maron et al., 2006; Ellis et al., in press).

Specifically, we examine differential growth and nutrient responses of four tropical tree species to experimental guano additions (low, medium, and high levels) in a controlled nursery environment. The four species selected—*Cocos nucifera* (Arecacea), *Pisonia grandis* (Nyctaginaceae), *Scaevola sericea* (Goodenaceae), and *Tournefortia argentea* (Boraginaceae)—are each from a different family and include one monocot (*C. nucifera*) and three dicots. These trees co-occur throughout many of the islands of the Central Pacific, where high abundances of tree-nesting seabirds live (Dombois and Fosberg, 1988). The particular species were chosen because of their dominance in this region and because of the established differences in their degree of association to seabirds. Seabirds are commonly associated with three of these four species (Clark et al., 1990; Megyesi and Griffin, 1996), whereas one species, the coconut palm (*C. nucifera*), provides poor nesting and roosting habitat for seabirds and is thus associated with low seabird abundance (Young et al., 2010a). Given previous observations of the distributional patterns of these four tree species along gradients of tree-nesting seabird abundance, we hypothesized that (1) the species that is not found in association with seabirds (i.e., *C. nucifera)* would have functional traits more associated with low-nutrient, stress-tolerant strategies (low SLA, low chlorophyll, low foliar nutrients) than would the other seabird-associated species (i.e., *P. grandis*, *S. sericea*, *T. argentea*), and (2) *C. nucifera* would have reduced performance responses (growth, chlorophyll, SLA) to fertilization, but would have similar responses in foliar nutrients.

MATERIALS AND METHODS

Greenhouse experimental conditions—Each of the four selected species was grown from seed in a greenhouse. Plants were grown in the same potting soil until the plants were no longer determined to be using seed resources. For the three seabird-associated species (*P. grandis*, *S. sericea*, and *T. argentea*), this occurred at 75 d, at which time the seed was no longer observable, and the plants all had at least 5 true leaves. For *C. nucifera*, the plant was deemed to be independent from its seed resources at 1 yr of age, at which time the seeds no longer contained liquid endosperm, and the plants had at least four fronds. At this time, all plants (69 of each seabird-associated species and 60 of *C. nucifera*) were removed from planting pots, and potting soil was rinsed clean from the roots. Plants then were replanted in 55 l pots (40 cm in height) in a 1 : 1 mixture of perlite and washed beach sand and were placed under controlled conditions (16-h light period, mean of 24°C). Plants were randomly assigned to high, medium, or low guano treatments, with 23 individuals of each species in each treatment. Commercially available seabird guano (12% N, and 12% P) was added 3 times per week, at a rate of 0.1 g per week in the low treatment, 1.0 g per week in the medium treatment, and 4.0 g per week in the high treatment. These treatment levels were selected to mimic the natural range of bird guano additions measured in Central Pacific forest sites. Low treatments are typical of those in *C. nucifera*–dominated low-bird sites, medium treatments are typical of sites dominated by *P. grandis* and *T. argentea* (although not dominant in any site, *S. sericea* is also more common in these *P. grandis*– and *T. argentea*–dominated forests), whereas high treatments are representative of the highest bird guano dropping rates observed at any sites (Young et al., 2010a, b). All plants were automatically watered the same amount four times per day (total approximately 12 l/d). Other essential nutrients ($MgSO_4$, K_2SiO_3, Fe-HEDTA, $MnCl_2$ $ZnCl_2$, H_3BO_3, $CuCl_2$, Na_2MoO_4) were hand mixed and delivered with the water supply equally across all treatments. Seabird-associated species were grown for a period of 75 d after transplantation. *Cocos nucifera* plants were grown for an additional 100 d to allow this species additional time to respond to treatments. During the course of the experiment, the plants were randomly moved three times to different positions within the greenhouse to reduce potential effects of microsite variation in light or temperature.

Plant growth—We used change in leaf biomass over time as our primary metric of growth. To nondestructively estimate this metric over the course of the experiment, we measured the length of all leaves (or fronds for *C. nucifera*). Using the length and mass of leaves from plants not involved in the experiment (minimum of 45 leaves per species), we developed leaf length–to–dry weight conversion factors that we used to estimate foliar biomass of growing plants. Leaf measurements were taken at 0, 30, and 75 d for all species. At the end of the experiment (75 d post transplantation for seabird-associated species, and 175 d post transplantation for *C. nucifera*), all plant material was harvested, and biomass was measured directly. For all plants, aboveground biomass was divided into foliar tissue and stem/rachis tissue, dried for 72 hr at 60°C, and weighed. Unless otherwise indicated, all discussion and analyses of aboveground biomass in this report refer to this final direct biomass measurement.

Belowground biomass was measured only at the time of harvest. The sand and perlite were washed from belowground root material at the time of harvest, and the material then was recleaned by hand after roots had been dried. Belowground tissue was dried for 7 d at 50°C. Belowground biomass was measured for all individuals of *C. nucifera* and *P. grandis* but only for a subset (7 individuals per treatment) of *S. sericea* and *T. argentea.* Shoot-to-root ratio was calculated as (total aboveground biomass) / (belowground biomass).

Foliar nutrients, SLA, and chlorophyll—Just before final harvest, we removed and stored frozen a 10 × 5 cm section of leaf area from the first fully extended leaf of each plant. Chlorophyll a and b levels were measured in these samples by using spectrophotometer measurements of foliar tissue in acetone (Porra et al., 1989). Chlorophyll levels are reported here as total chlorophyll (a + b) per mg dry weight. Specific leaf area was determined by taking the dry weight of a known area of leaves. For foliar nutrients, all the remaining laminar tissue was washed, oven dried (60°C), and milled (2 mm mesh). Foliar P was determined by using Kjeldahl digestions, followed by analysis on a continuous-flow autoanalyzer (Alpkem Flow Solution IV, Stanford University, Stanford, California, USA). Foliar C and N were estimated with the use of a C/N analyzer (Carlo Erba 1500, Stanford University).

Data analysis—We used multiple analyses of variance (MANOVA) to compare plant functional traits (final aboveground biomass, % foliar P, % foliar N, % foliar C, SLA, chlorophyll, and shoot-to-root ratio) both across species and across treatments within species (for *P. grandis*, MANOVA across treatments within species did not include SLA because of low sample size for this trait in this species). Before MANOVA, data sets were tested for normality with a Mardia test of multinormality and, when necessary, were Box-Cox transformed to normalize distributions; they subsequently were checked for homogeneity of variances. Following significant whole model MANOVAs, comparisons across species or treatment were made by using analyses of variance (ANOVA) with subsequent Tukey-Kramer post hoc pairwise comparisons.

Belowground biomass was not considered in the MANOVA, as it was not measured in all plants (small sample size for two species), but it was analyzed separately as an ANOVA. To examine interaction effects between species and fertilization treatment of our primary metric of growth (foliar biomass) at 0, 30, and 75 d, we used a generalized linear model procedure (GLM). All statistics were computed in JMP 8 (SAS Institute, Cary, North Carolina, USA). The figures and table depict untransformed data, and all mean values are shown with standard deviation unless otherwise noted.

RESULTS

Comparison of the five functional traits between species showed that species were indeed functionally different from one another (MANOVA Wilks' lambda = 0.006, $F_{21,230}$ = 53.33, $P < .0001$; univariate results in Table 1). Within-species analysis of plants exposed to different rates of guano addition showed that each also responded in a significantly different fashion (within this suite of traits) (MANOVA: *C. nucifera*, Wilks' lambda = 0.150, $F_{12,92}$ = 12.15, $P < .0001$; *S. sericea*, Wilks' lambda = 0.100, $F_{12,78}$ = 14.0, $P < .0001$; *T. argentea*, Wilks' lambda = 0.1000, $F_{12,96}$ = 17.19, $P < .0001$; *P. grandis*, Wilks' lambda = 0.107, $\mathrm{F}_{10,114}$ = 23.5, $P < .0001$).

Growth and biomass—Examining the effects of species and fertilization treatment on foliar biomass, we found that by 30 d (but not before), species, treatment, and species × treatment interaction all showed significant effects on foliar biomass (species $P < .001$, treatment $P < .01$, species × treatment $P < .05$). All factors remained significant at 75 d.

To examine the cause of the interactive species × treatment effects, we then examined response to fertilization within species. We found that *C. nucifera* showed no differences in foliar biomass among treatments at any point in the experiment (Figs. 1A, C, and Fig. 2; final foliar biomass ANOVA $F_{2,60}$ = 0.50, P = .61). In contrast, for all seabird-associated species, differences began to emerge over time (Figs. 1D–F). At 75 d, foliar biomass was significantly different for all seabird-associated species (ANOVA: *P. grandis*, $F_{2,66}$ = 4.48, P = .01; *S. sericea*, $F_{2,64}$ = 15.59, $P < .0001$; *T. argentea*, $F_{2,65}$ = 3.66, P = .03). Whereas the degree of change and patterns of significance in post hoc pairwise comparisons varied somewhat among species, all seabird-associated species showed significant increases in foliar biomass from low to medium treatments (Fig. 2). Only two of the species had any mortality during the experiment: *S. sericea* had 12% mortality (all in high treatments), and *T. argentea* experienced 22% mortality (also only in high treatments).

With regard to belowground biomass metrics, *C. nucifera* did not show any difference in final belowground biomass across fertilization treatments. In contrast, two of the three seabird-associated species showed significant differences in final belowground biomass across treatments, though the direction of change across treatments varied between species, with *P. grandis* showing increased belowground biomass with increased nutrient additions, whereas *S. sericea* showed reduced belowground biomass with increased additions (Fig. 2; ANOVA: *P. grandis*, $F_{2,66}$ = 4.67, P = .01; *S. sericea*, $F_{2,20}$ = 5.11, P = .02). Shoot-to-root ratios were not significantly different across treatments within species.

Foliar nutrients—All species showed strong differences across treatments in both foliar N and foliar P at the end of the experiment (Fig. 3). Foliar N of all four species showed strong sequential increases from low to medium and medium to high treatments (Table 1). *Cocos nucifera* had a mean of 32% change from low to high treatments (ANOVA: $F_{2,55}$ = 83.8, $P < .0001$). *Pisonia grandis* had a mean of 87% change from low to high treatments (ANOVA: $F_{2,57}$ = 133.88 $P < .0001$). *Scaevola sericea* had a mean of 51% increase in foliar N from low to high treatments (ANOVA: $F_{2,59}$ = 105.52, $P < .0001$). Finally, *T. argentea* had a mean of 127% increase in foliar N from low to high treatments (ANOVA: $F_{2,49}$ = 116.2, $P < .0001$). Similarly, foliar C : N showed a sequential decrease as seen in foliar N across treatments for all species (ANOVA: *C. nucifera*, $F_{2,55}$ = 101.3, $P < .0001$; *P. grandis*, $F_{2,57}$ = 78.9, $P < .0001$; *S. sericea*, $F_{2,57}$ = 84.5, $P < .0001$; *T. argentea*, $F_{2,59}$ = 84.7, $P < .0001$).

Foliar P also showed strong differences among treatments for all four species, though the increase in foliar P generally occurred only at high treatment levels (Fig. 3). *Cocos nucifera* had a 32% increase in foliar P from low to high treatments (ANOVA: $F_{2,55}$ = 33.97, $P < .0001$). *Pisonia grandis* had a 10% increase from low to high treatments (ANOVA: $F_{2,57}$ = 6.77, $P < .01$). *Scaevola sericea* had a 110% increase in foliar P (ANOVA: $F_{2,59}$ = 38.06). Lastly, *T. argentea* had a 150% increase in foliar P from low to high treatments (ANOVA: $F_{2,49}$ = 19.05).

Chlorophyll—*Cocos nucifera* showed no differences in total chlorophyll (a and b) levels among fertilization treatments (ANOVA: $F_{2,52}$ = 0.12, P = .87; Fig. 4). However, each of the three seabird-associated species showed strong differences in chlorophyll between treatments, with each species having higher chlorophyll in high and or medium treatments than in low treatments, though the degree of change across treatments differed somewhat among species (Fig. 4). Mean differences (comparing low to high) among treatments for each species was 59% for *P. grandis*, 28% for *S. sericea*, and 29% for *T. argentea* (ANOVA: *P. grandis*, $F_{2,62}$ = 9.27 $P < .001$; *S. sericea*, $F_{2,49}$ = 12.05, $P < .0001$; *T. argentea*, $F_{2,44}$ = 27.48, $P < .0001$).

Specific leaf area—*Cocos nucifera* showed no difference in SLA among treatments. In contrast, two seabird-associated species showed significant differences among treatments (*S. sericea*, $F_{2,44}$ = 3.63, P = .03; *T. argentea*, $F_{2,56}$ = 4.50, P = .02). For *S. sericea*, SLA was highest in medium-nutrient treatments (196.8 ± 23.9 cm^2/g); these SLA levels were significantly elevated over

TABLE 1. Comparison of selected functional traits across species pooled by fertilization treatment (mean ± SD). Letters show significant pairwise differences; species with the same letters (within a trait) are not significantly different.

Trait	*F* (*P*)	*Cocos nucifera*	*Pisonia grandis*	*Scaevola sericea*	*Tournefortia argentea*
% Foliar phosphorus	111.9 (<0.001)	0.18 ± 0.03 (A)	0.30 ± 0.06 (B)	0.21 ± 0.11 (A)	0.32 ± 0.12 (B)
% Foliar nitrogen	162.6 (<0.0001)	1.51 ± 0.30 (A)	3.78 ± 0.85 (B)	2.81 ± 1.02 (C)	4.64 ± 1.58 (D)
Foliar C : N	32.5 (<0.001)	32.83 ± 0.57 (A)	10.92 ± 0.57 (B)	16.15 ± 0.59 (C)	9.91 ± 0.60 (B)
SLA (cm^2/g)	175.6 (<0.0001)	128.88 ± 8.12 (A)	245.01 ± 0.85 (B)	182.98 ± 28.26 (C)	210.97 ± 52.05 (B)
Chlorophyll (a + b) / mg dry weight	196.5 (<0.0001)	1.82 ± 0.74 (A)	3.85 ± 1.60 (B)	2.87 ± 0.57 (C)	4.41 ± 1.14 (D)
Aboveground / belowground biomass	116.0 (<0.001)	0.6 ± 0.1 (A)	1.1 ± 0.4 (B)	2.9 ± 1.1 (C)	1.6 ± 0.6 (D)

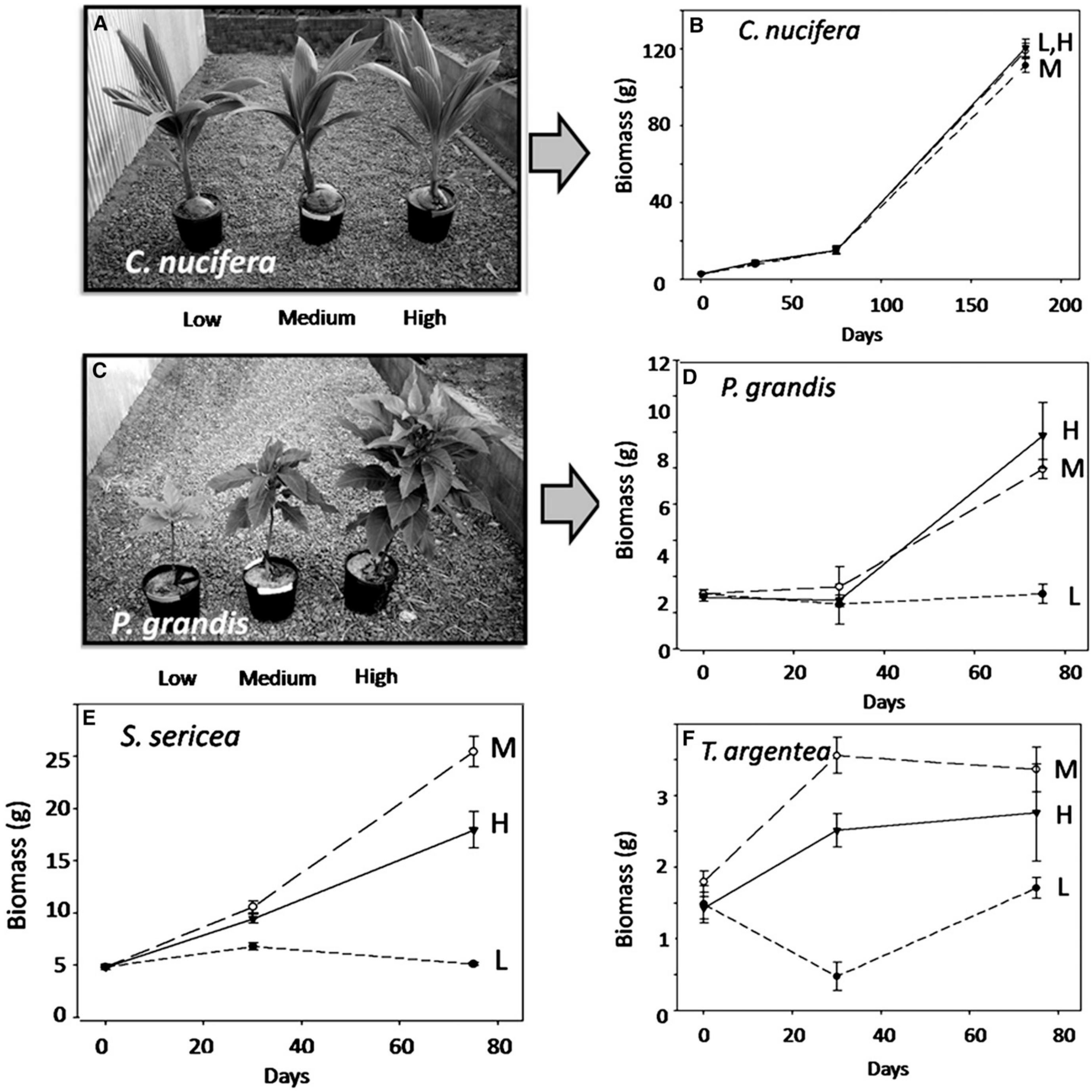

Fig. 1. Differences in growth across species. Panels A and C show images of largest individuals of *Cocos nucifera* and *Pisonia grandis*, respectively, under each treatment at the time of final harvest. Although no clear differences are visible in size or chlorophyll levels in *C. nucifera* individuals across treatments in the photos, differences in total size and chlorophyll levels were different, as can clearly be seen in *P. grandis*. The corresponding data, showing time course of foliar biomass (mean ± SE) for *C. nucifera* and *P. grandis* in each treatment, are seen in panels B and D, respectively. Panels E and F show the same data for the other two species studied, *Scaevola sericea* and *Tournefortia argentea*. Treatments are marked as high (H), medium (M), or low (L) fertilization. No significant effects of treatment of *C. nucifera* exist at any point; all other species show significant effects of treatment after 75 d.

high (172.9 ± 25.4 cm^2/g) and low nutrient treatments (184.3 ± 23.3 cm^2/g). Likewise, SLA for *T. argentea* was also highest in medium-nutrient treatments (236.1 ± 51.8 cm^2/g); however, this was significantly elevated over only high (191.6 ± 52.3 cm^2/g) treatments and not low treatments (203.9 ± 48.8 cm^2/g). Specific leaf area was not compared across treatments for *P. grandis.*

DISCUSSION

As would be expected given their highly divergent phylogenetic backgrounds, the four species examined have very different functional traits. *Cocos nucifera,* the only monocot, had the lowest foliar N, foliar P, SLA, and chlorophyll. It also had the

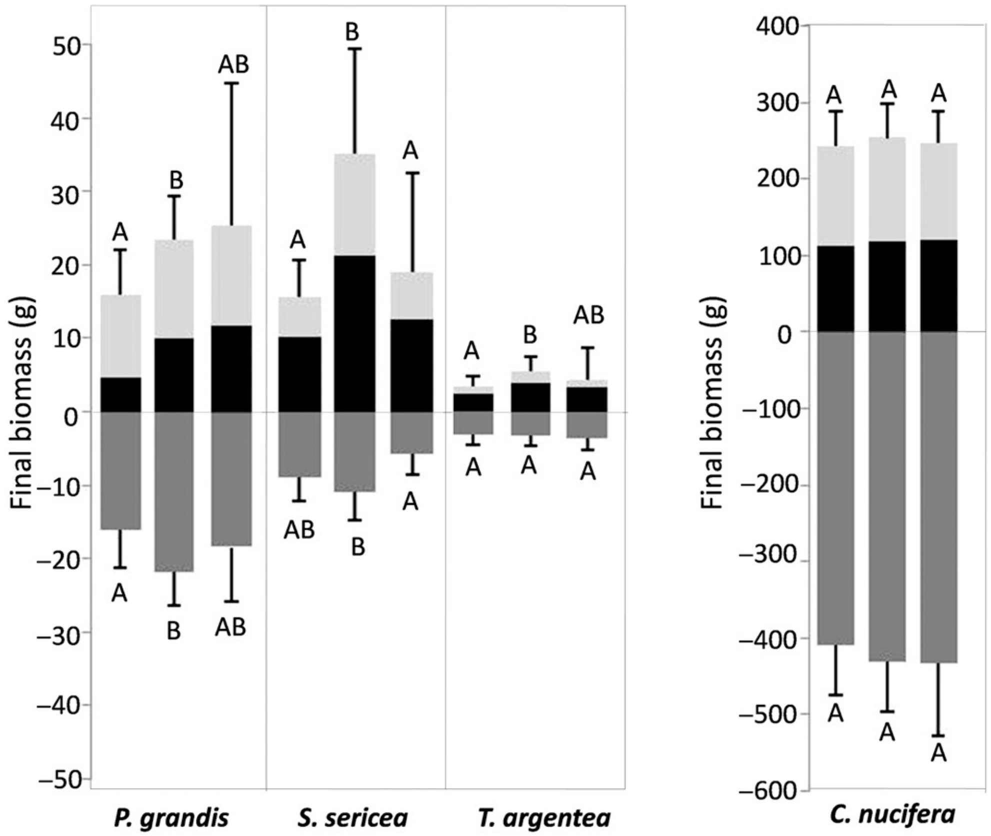

Fig. 2. Final foliar (light gray), stem (black), and belowground (dark gray) biomass across treatments for each of the four species: *Pisonia grandis*, *Scaevola sericea*, *Tournefortia argentea*, and *Cocos nucifera*. Biomass is final dry biomass, measured destructively at the end of the experiment (175 d for *C. nucifera*, 75 d for all other species). Error lines depict standard deviation for total aboveground biomass (combined foliar and stem biomass) and total belowground biomass. Letters show significant pairwise differences; treatments with the same letters (within species) are not significantly different.

highest C : N ratio and the lowest shoot-to-root ratio of all species. This suite of traits is characteristic of monocots and is also characteristic of stress-tolerant plants found in low-nutrient environments (Tilman, 1988; Chapin et al., 1993). It is thus not surprising that this species is able to thrive in the low-bird conditions it creates (as birds do not use it for nesting or roosting; Young et al., 2010a). In contrast, the bird-associated species all appear to have functional traits that maximize the potential for rapid resource capture (fine structure, high foliar N, high chlorophyll) typical of competitor species (Grime, 2001). Within these three bird-associated species, no consistent ranking existed with respect to the functional traits.

Given the high variability in functional traits and the taxonomic uniqueness of these species, we expected strong variation in responses of traits to guano fertilization across species. As hypothesized, the monocot *C. nucifera* showed few major responses to nutrient addition. It showed no changes in aboveground or belowground biomass, chlorophyll, or SLA across nutrient treatments. This differed considerably from all other species, which showed significant increases in each of these variables at either or both medium- and high-nutrient treatments compared with low-nutrient treatments. It may be that *C. nucifera* has relatively low plasticity in this suite of traits.

The only functional trait for which *C. nucifera* showed significant response to fertilization was in foliar nutrients. Foliar N and foliar P showed substantial increases with nutrient addition. This is also consistent with plant strategy predictions, as stress-tolerant species often accumulate reserves of nutrient elements in times of resource availability to cope with stressful nutrient conditions at later times (Clarkson, 1967; Grime, 2001).

In contrast to the lack of observed difference in relative growth rates across treatments for *C. nucifera*, the relative growth rates of the other three species did respond to guano additions, including a more than 100% increase in foliar biomass across treatments for *S. sericea* and more than 65% for *P. grandis.* Notably, most of the increase in biomass for these species was between low and medium treatments, and no further significant increases in biomass occurred from medium to high treatments. Indeed, *S. sericea* actually had significant declines in aboveground biomass from medium to high treatments. Both *S. sericea* and *T. argentea* also experienced some mortality in high treatments. It seems likely that the very high treatments may have corresponded to levels toxic to these species. The level of foliar nutrients accumulated by these two species continued to increase with increased fertilization, perhaps to levels that were detrimental to plant growth, as seen in other experiments (i.e., Jones, 1974). Additionally, the acidity of the guano also may have contributed to this mortality. *Pisonia grandis*, in contrast, showed no negative declines in foliar biomass at high guano treatments, and its chlorophyll levels were actually significantly elevated. This is consistent with research on *P. grandis* that suggests it thrives in sites with very high densities of seabird, even in acidic guano environments (Shaw, 1952; Walker, 1991, Burger, 2005). There also appears be a relation between

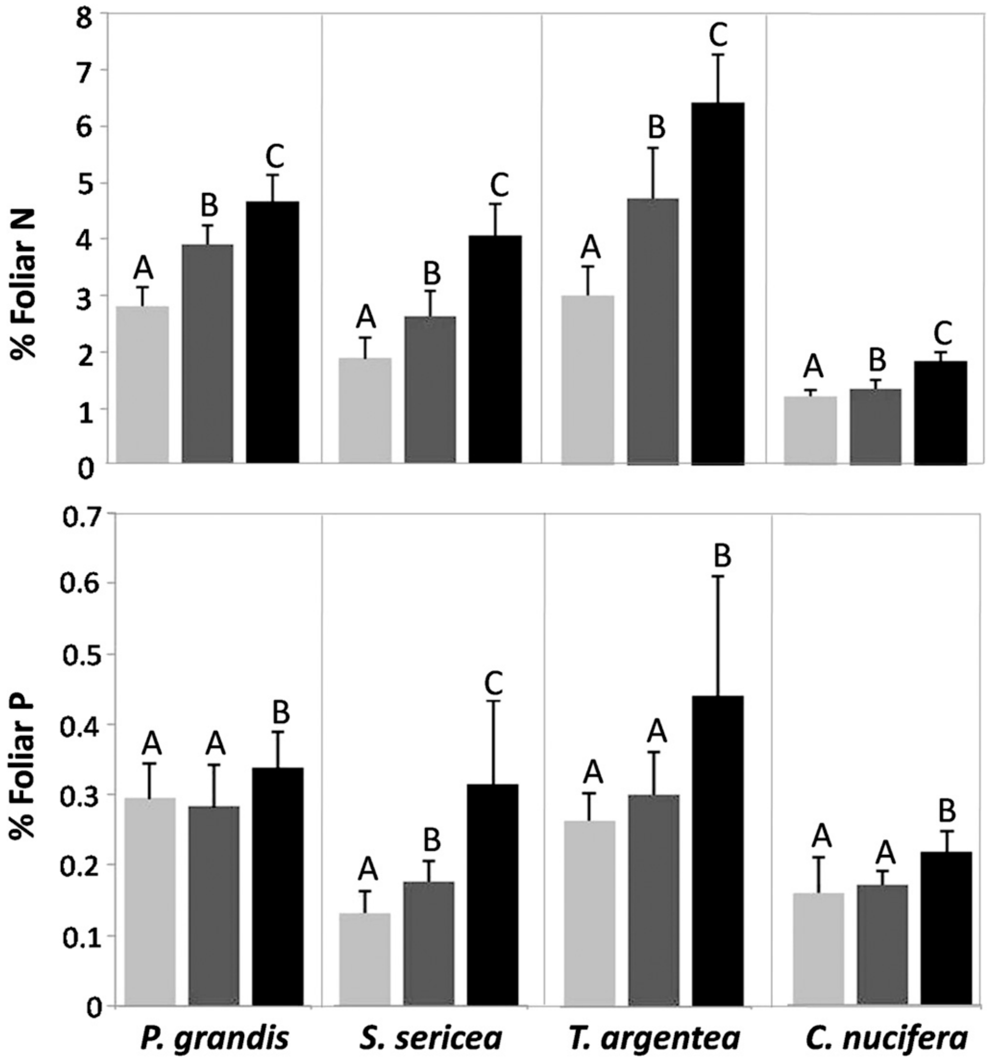

Fig. 3. Percent foliar nitrogen (N) and percent foliar phosphorus (P) (mean with SD) across low (light gray), medium (dark gray), and high (black) guano addition treatments for each of the four species: *Pisonia grandis*, *Scaevola sericea*, *Tournefortia argentea*, and *Cocos nucifera*. Letters show significant pairwise differences; treatments with the same letters (within species) are not significantly different.

growth response to guano addition and mortality in high treatments, suggesting that some gradient of adaptation/tolerance may exist among these seabird-adapted species, though more field data would be needed to confirm this.

In summary, it appears that *C. nucifera* has different functional traits than seabird-associated species common in this system (Table 1). More notably, it also showed reduced responses to fertilization as compared with the other seabird-associated species common in this system. Of the three seabird-associated species, *P. grandis* is somewhat distinct in that it appears to be generally resistant to guano toxicity, experiencing no mortality or negative changes in performance at highest guano additions. The stronger responses to bird guano, in terms of growth, chlorophyll, and SLA response of seabird-associated species, as compared with *C. nucifera*, are consistent with expectations based on life history traits. Bird-associated species appear to have traits and growth responses characteristic of competitive species adapted to maximize short-term growth, whereas *C. nucifera* has traits more associated with enhancing nutrient conservation. The only measured trait that did not match predictions was shoot-to-root ratio, for which no significant effect of treatment was seen across any species. These differences should allow native seabird-associated species to perform better relative to *C. nucifera* in productive sites typical of many of these bird colonies.

This study only directly tests functional traits and growth responses of juvenile plants; however, given that the establishment period frequently has naturally high mortality, this is likely a critically important response period in plant ontongeny. Furthermore, for the subset of these traits that also have been measured in adult plants in the field (SLA, foliar nutrients), similar results have been found, suggesting that these conclusions also hold for adult plants (Young et al., 2010a). This study also likely under-represents the differential abilities of these species to establish in low-nutrient environments, as the large nut resources of *C. nucifera* would likely give them further advantages in establishment in low-nutrient situations. Because the *C. nucifera* that thrived in our laboratory-created low-nutrient conditions had already exhausted their nut resources, we expect them to do even better in nutrient-depleted field conditions when they can draw from these seed resources.

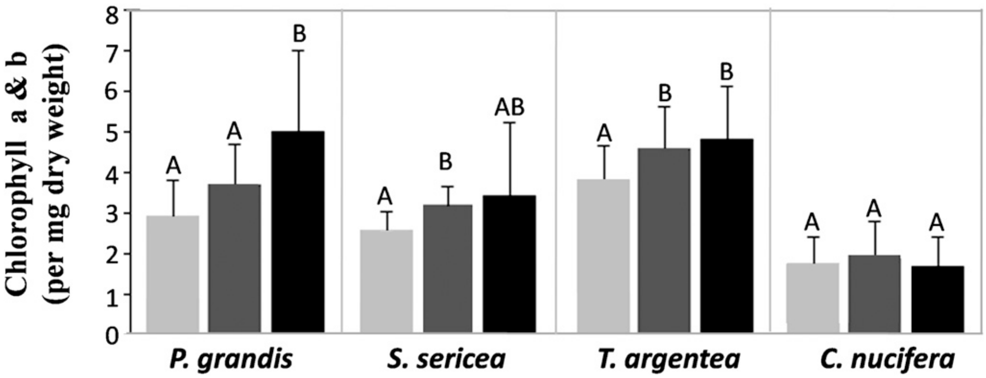

Fig. 4. Total chlorophyll (chlorophyll a + b; mean with SD) across low (light gray), medium (dark gray), and high (black) treatments for each of the four species: *Pisonia grandis*, *Scaevola sericea*, *Tournefortia argentea*, and *Cocos nucifera*. Letters show significant pairwise differences; treatments with the same letters (within species) are not significantly different.

The results of this study clearly document the potential for highly divergent responses across plant species to guano or other nutrient additions. Although the results from this study also support the suggestion that systematic changes in plant community composition along gradients of seabird abundance may be correlated to variation in plant functional traits, additional studies comparing a larger suite of species, ideally including species that are taxonomically related, will confirm this mechanistic link.

These results are also pertinent to those working in the field of invasion biology, particularly in the Pacific region. *Cocos nucifera* was likely introduced in much of its current range by humans and probably has expanded considerably since then (Ward and Brookfield, 1992; Baudouin and Lebrun, 2009). Our findings thus provide an important example of how an introduced species with a life history strategy similar to those of stress-tolerant species can gain a performance advantage over native species in low-nutrient environments. This is in contrast to most invasive or range-expanding plants, which tend to have high foliar N, high chlorophyll levels, high shoot-to-root ratios, and high SLA (van Kleunen et al., 2010). Likewise, most introduced plants that alter nutrient cycles do so by increasing soil nutrients (Vitousek, 1997; Vitousek and Walker, 1989; Lindsay and French, 2005); however, the presence of *C. nucifera* can actually create low-nutrient environments by disrupting seabird subsidies. The mechanisms that have facilitated the success of this palm serve as a useful model for understanding the biochemical or functional origins of invasion success in other plant species.

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