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SHORT COMMUNICATION

Within-species leaf trait variation and ecological flexibility in resprouting tropical trees

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Plants have an inherent flexibility to respond to different environmental conditions. One axis of plant ecophysiological strategy is seen in the spectrum of leaf functional traits. Flexibility in these traits would be suggestive of plants' phenotypic plasticity in response to environmental changes. This research seeks to identify differences between leaves of sprout and non-sprout shoots of a broad ecological range of neotropical tree species. Using a functional-trait approach, this study assesses a large pool of species for within-species physiological flexibility. Leaf mass per area (LMA) and leaf area were measured for plants of sprout and non-sprout origin for 26 tree species grown in a reforestation plantation in Panama. Sprouts had a consistently lower LMA than non-sprouts, but there was no consistent pattern for leaf area. These trends show that sprouts are more like pioneer species than conspecific saplings, a finding in general agreement with fast sprout growth seen in previous studies. Further, later-successional (high LMA) species showed a greater reduction of LMA in sprouts. These results show that tropical tree species adjust physiologically to changing ecological roles and suggest that certain species may be more resilient than realized to changing climate and disturbance patterns.

Sprouting following disturbance is common in most woody plant-dominated ecosystems (Bond & Midgley 2001). Sprouts grow faster than conspecific saplings (Dietze & Clark 2008), due in part to mobilization of stored carbohydrates (Luostarinen & Kauppi 2005), but differences between shoot and sprout leaves may also accelerate sprout growth. Physiological differences between sprout and non-sprout leaves have been shown for a few species (Donovan & Pappert 1998, Kruger & Reich 1993), but I am unaware of any study that has investigated such patterns more broadly. This study uses leaf mass per area (LMA) as a proxy for plant ecophysiological differences. Increased LMA is associated with slower-growing, shade-tolerant species, and is clearly correlated with increased leaf lifespan, resistance to mechanical damage and decreased photosynthetic capacity (Kitajima & Poorter 2010, Wright *et al.* 2004). Low-LMA leaves are found on faster-growing, light-demanding species (Coley 1980).

The aim of this study is to test the hypotheses (1) that sprout LMA will decrease relative to that of conspecific saplings, in both cases showing trends toward values more typical of pioneer species and (2) that later-successional species will have a greater phenotypic flexibility when recovering from damage. Because leaf traits vary due to genotype, environment, plant age and leaf age (Augspurger *et al.* 2005, de Casas *et al.* 2011), this study's design compares sprouts and saplings with minimal differences in these attributes for neotropical tree species with a wide range of life-history strategies.

All study plants were grown in a forestry trial plantation in Soberania National Park, Panama located at 9°06′N, 79°37′W and about 150 m asl. The plantation was established in 2003–2004 by PRORENA, the Native Species Reforestation Project of the Smithsonian Tropical Research Institute and Yale University. The site has an average rainfall of 2100 mm y^{-1}, a dry season of about

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Table 1. Details of study species and P-values of leaf mass/area (LMA) differences among trees and sprouts of 26 neotropical species. The P-values are for two-tailed t-tests. For LMA, all significant differences were in the direction of having lower values of LMA in sprout leaves. The column n gives the total number of leaf samples on which area and LMA were measured. Samples were typically split evenly between sprouts and trees, although occasional odd numbers result from lost or damaged samples. The numbers in the first column reference the numbered points in Figure 1.

	Species	Family	Year planted	LMA P	Sprout/tree leaf size ratio	Leaf area P	n
1	*Albizia adinocephala* (Donn. Sm.) Britton & Rose	Fabaceae	2003	0.023	1.11	0.593	30
2	*Albizia guachapele* (Kunth) Dugand	Fabaceae	2003	< 0.001	1.43	0.019	24
3	*Byrsonima crassifolia* (L.) Kunth	Malpighiaceae	2004	< 0.001	1.04	0.746	24
4	*Calycophyllum candidissimum* (Vahl) DC.	Rubiaceae	2003	0.085	1.16	0.329	24
5	*Colubrina glandulosa* (Perkins)	Rhamnaceae	2003	< 0.001	0.78	0.278	24
6	*Cordia alliodora* (Ruiz & Pav.) Oken	Boraginaceae	2003	0.033	0.95	0.835	12
7	*Dalbergia retusa* (Hemsl.)	Fabaceae	2004	< 0.001	0.95	0.489	36
8	*Diphysa americana* (Mill.) M. Sousa	Fabaceae	2003	0.280	1.57	< 0.001	36
9	*Erythrina fusca* Lour.	Fabaceae	2003	0.001	1.41	0.028	24
10	*Gliricidia sepium* (Jacq.) Kunth ex Walp.	Fabaceae	2003	0.157	0.91	0.363	36
11	*Guazuma ulmifolia* Lam.	Sterculiaceae	2003	< 0.001	1.77	0.001	24
12	*Hura crepitans* L.	Euphorbiaceae	2004	0.851	0.93	0.676	24
13	*Hymenaea courbaril* L.	Fabaceae	2004	< 0.001	0.75	0.031	24
14	*Inga punctata* Willd.	Fabaceae	2003	0.003	0.84	0.280	36
15	*Luehea seemannii* Triana & Planch.	Tiliaceae	2003	< 0.001	1.65	0.004	24
16	*Ormosia macrocalyx* Ducke	Fabaceae	2004	< 0.001	1.07	0.623	36
17	*Pithecellobium longifolium* (Humb. & Bonpl. ex Willd.) Standl.	Fabaceae	2004	0.006	0.84	0.436	12
18	*Samanea saman* (Jacq.) Merr.	Fabaceae	2003	< 0.001	1.01	0.932	18
19	*Sapindus saponaria* L.	Sapindaceae	2004	< 0.001	1.40	0.031	36
20	*Spondias mombin* L.	Anacardiaceae	2003	0.545	0.58	0.002	21
21	*Swietenia macrophylla* King	Meliaceae	2004	< 0.001	1.81	0.011	23
22	*Tabebuia guayacan* (Seem.) Hemsl.	Bignoniaceae	2003	0.017	0.90	0.353	69
23	*Tabebuia rosea* (Bertol.) A. DC.	Bignoniaceae	2003	0.004	0.64	0.120	24
24	*Tabebuia impetiginosa* (Mart. ex DC.) Standl.	Bignoniaceae	2004	0.034	0.91	0.432	36
25	*Tectona grandis* L.f.	Verbenaceae	2003	0.888	1.17	0.343	36
26	*Terminalia amazonia* (J.F. Gmel.) Exell	Combretaceae	2003	< 0.001	1.26	0.002	72

4.1 mo from around December to April and moderately fertile soil (Craven *et al.* 2007). The site is dominated by an exotic grass, *Saccharum spontaneum* L., which has been regularly cut since planting. For a more detailed site description, see Craven *et al.* (2007).

In 2003 and 2004 nine replicated blocks of each of 70 tree species were planted by PRORENA. Most of these are native to Panama, although a few common tropical plantation species were included for comparison. Each block consisted of 20 greenhouse-germinated seedlings in a 5×4 grid with 3 m between adjacent plants. These were grown from seeds collected mostly from wild-growing parents, although parentage of individual seedlings was not tracked. The blocks were thinned 2 y after planting so that ten live plants remained. Removed saplings were cut a few cm above ground level, and stumps were left undisturbed. Any sprouts that grew from the stumps were not cut. Hereafter uncut plants are referred to as 'saplings' and regrowth from cut stumps as 'sprouts'.

In February 2007, leaves were collected from saplings and sprouts of the 26 species (Table 1) that sprouted in sufficient numbers. Three leaves (or leaflets from compound leaves) were collected from each sampled plant, mostly between 1–2 m above the ground. While it was impossible to determine the exact age of leaves sampled, nearly all of these species grow leaves in synchronous flushes, and all leaves were sampled from near the end of active twigs, ensuring that leaf age was similar between sprouts and saplings of a particular species. Plants within a block were chosen randomly, and selected leaves were well exposed to sun and not visibly damaged. On branched plants, leaves were collected from separate twigs. Multiple leaflets were never collected from a single leaf. Because sprouts were generally shorter than non-sprouts, all sampling focused on the edges of blocks to obtain leaves of similar exposure, and in most cases, from similar heights above the ground. Plant heights at the time of collection varied with species' growth rates, but most were between 1 and 10 m tall. Leaves were transported to the laboratory in plastic bags and measured with a Li-Cor LI-3100C leaf area meter within 1 d of collection. Measurements excluded petioles and the petiolules and rachises of compound leaves. Following area measurement, all leaves were immediately placed in a plant press and dried at 100 °C. Dried leaves were weighed on an electronic balance. Trait differences were assessed using two-tailed t-tests in R (R Foundation for Statistical Computing, Vienna, Austria).

Leaf mass per area ranged from 0.0027 g cm^{-2} for sprouts of *Albizia guachapele* to 0.014 g cm^{-2} for saplings

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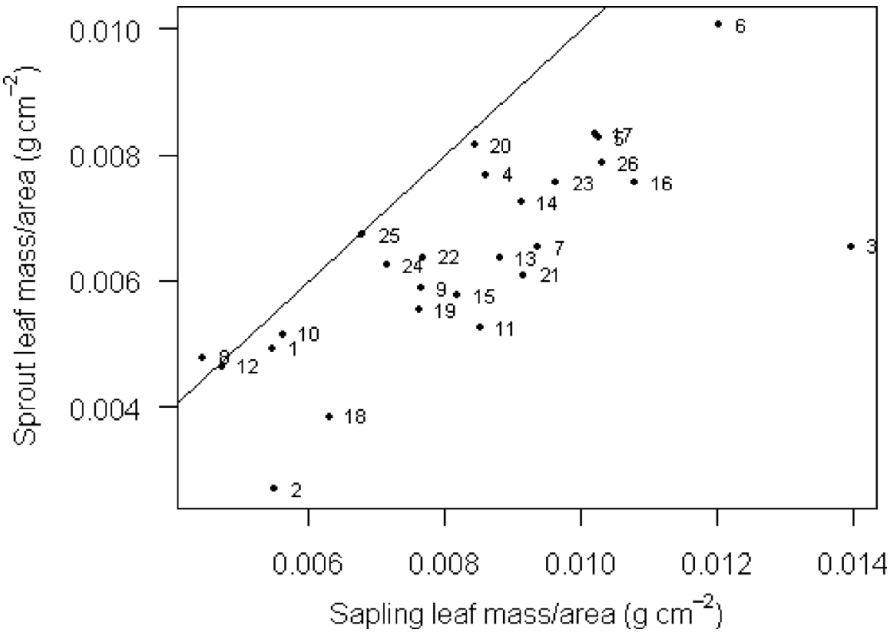


Figure 1. Leaf mass per area for saplings and sprouts of 26 tree species grown in a plantation in Soberania National Park in Panama. The diagonal line is a 1:1 line. Each point refers to a single species. The numbers refer to species in Table 1.

of *Byrsonima crassifolia*. All but one of the 26 species had a lower mean LMA in sprouts than in saplings (Figure 1). Results of two-tailed t-tests show that in most cases these differences were unlikely to be due to chance (Table 1). Of the 26 species, 20 reached the $P < 0.05$, all in the direction of higher LMA on saplings (Table 1). Saplings with a higher sapling LMA showed a strong trend toward greater reduction of LMA as sprouts ($P = 0.00005$, $R^2 = 0.502$). When phylogenetically independent contrasts were used to take relatedness of the species into account, this relationship remained virtually unchanged (data not shown). Qualitatively similar, although weaker, results were seen for the proportionate reduction of LMA as a function of sapling LMA ($P = 0.025$, $R^2 = 0.191$). For leaf size, 10 out of 26 species had significant ($P < 0.05$) differences between sprouts and saplings, with no directional trend (Table 1).

This study has shown pervasively lower LMA in sprout leaves compared with conspecific sapling leaves. Not all species were equal in their ability to make such adjustments. Late-successional species with high LMA on undamaged plants showed a much greater flexibility to decrease LMA than sprouts. To my knowledge, no previous study has shown such trends in a diverse array of species. Not only are these trends consistent across species, but they are also consistent with one another, as predicted by cross-species comparisons of leaf traits in large datasets of diverse plant species (Wright *et al.* 2004).

The finding of pervasive changes in sprout functional traits is qualitatively consistent with previous studies of sprouting. Sprouts tend to have more juvenile characteristics, such as indeterminate growth, than shoots of mature plants (Del Tredici 2001). In both tropical (Mostacedo *et al.* 2009) and temperate (Dietze & Clark 2008) forests, sprouts grow faster than conspecific non-sprouts. Put in other words, sprouts are more pioneer-like than undamaged plants of the same species. Pioneer species tend to have lower LMA (Reich *et al.* 2003), much like those measured sprouts in this study. While the faster growth of sprouts is probably due in part to remobilization of carbohydrates from roots (Luostarinen & Kauppi 2005), the pattern shown here is an additional facet of sprouting behaviour.

At first glance, the finding that saplings with high LMA have more flexibility to reduce their LMA as sprouts appears obvious: a large value can be reduced more than a smaller one while still constructing a viable leaf. However, the realization of this possibility has complex implications. High LMA and its accompanying traits in the leaf economic spectrum are adaptations to low light typically experienced by late-successional species. Such species are less likely to seed into gaps, but more likely to be a pre-existing part of the understorey when a treefall gap opens. This is an environment in which sprouting, and then adapting to and growing quickly in high light, would be a clear advantage.

This study has shown that functional traits are not an invariant property of species. Even so, a heightened understanding of leaf physiological constraints has come from studies treating such traits as a species-level property (Wright *et al.* 2004). Building on the basic understanding of leaf-level trait constraints, this study heightened

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understanding of the flexibility of tropical tree species in responding to changing conditions. These traits do vary within species, but in predictable ways constrained both by physiological trade-offs and demographic responses to disturbance. This shows a clear use for functional traits beyond their traditional role in describing species-level adaptations.

While this paper has documented a remarkable similarity among the studied tropical tree species, it is important to note that they represent only a subset of tropical biodiversity. While these species are ecologically and evolutionarily diverse, they share in common the ability to sprout. Other species in the same plantations rarely sprout under identical conditions (Salk & McMahon 2011). Thus, the results of this study support conclusions about physiological plasticity only for species that actually form sprouts. However, the broad ecological and phylogenetic spread of the species considered show that changes in leaf function are a critical part of the sprouting response of tropical trees.

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