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Seed weight and rooting depth of seedlings of Costa Rican wet forest trees

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Resumen: Se comparó el largo de la raíz y la tasa de crecimiento de las plántulas de nueve especies de árboles tropicales con semillas de tamaños diferentes, con el fin de probar la hipótesis de que las plántulas de semillas grandes emiten raíces más profundas que las pequeñas. El peso seco de la semilla estuvo débilmente correlacionado con el largo promedio de la raíz; la correlación entre peso seco de la semilla y el largo máximo de la raíz para cada especie fue aún mas débil, particularmente a los dos meses. En contraste, el tamaño de la semilla correlacionó inversamente y en forma significativa con la tasa relativa de crecimiento. A pesar de tener menos reservas almacenadas, las plántulas de especies de semillas pequeñas pueden extender sus raíces tan profundo como las especies de semillas grandes, como resultado de su rápido crecimiento y de sus raíces finas.

Key words: seed characteristics, root depth, Tropical forest.

Seed size has been frequently correlated with environmental conditions, habitat, or life form (Salisbury 1942, Baker 1972). Among trees, early-successional species usually have smaller seeds than late-successional species (Bazzaz & Pickett 1980, Putz 1983). Large seeds are thought to be advantageous in competitive or stressful environments because greater seed reserves permit seedlings to withstand periods when carbon acquisition is limited, for example by shade or drought (Baker 1972). Because their growth is derived from stored reserves as well as from current photosynthate, large-seeded species have been postulated to produce seedlings with deeper roots than those of small-seeded species, even when carbon acquisition is not limited (Baker 1972, Putz & Appanah 1987). As a consequence of deeper roots, large-seeded plants should be less affected by drought periods (subsequent to favorable establishment periods) than small-seeded plants. However, the link between large seeds and superior production of deep roots by seedlings has not been clearly shown. Root extension in small-seeded species might be as rapid as that of large-seeded species because small-seeded, early-successional species often have higher growth rates than large-seeded, late-successional species (Bazzaz & Pickett 1980). Furthermore, as seedlings, small-seeded species often have finer roots than large-seeded species and thus may obtain equivalent root depth with less biomass.

Tropical forests are logical sites for testing the relation between seed size and seedling rooting depth because for many tropical forests, a dry season presents a drought period in the midst of a predominantly mesic year. The need for a long seedling growth period before the dry season is thought to be an important selective force upon seed dispersal/germination of tropical species confronted with a dry season (Frankie, Opler & Bawa 1974). Rapid production of deep roots could be important for minimizing the severity of the dry season for tree seedlings.

In this report, the maximum root depth and growth rates of seedlings of nine tropical tree species with a range of seed sizes were compared in order to test the hypothesis that seedlings of large-seeded tree species have greater root extension than small-seeded species.

The study was conducted at the La Selva Biological Reserve (83° 59'W, 10° 26'N) in the Atlantic lowlands of Costa Rica. The forest at La Selva is classified as tropical wet and has an average annual rainfall total near 4000 mm.

Nevertheless, a distinct dry season occurs from January to April. Peak fruit production at La Selva occurs in September and October (Frankie, Opler & Bawa 1974); consequently, seeds of many species are dispersed within a few months of the onset of the dry season.

Seedlings of nine species (listed in Table 2) were grown for two months in deep containers to determine maximum root extension. Seeds of one of the nine species, *Ochroma lagopus*, were also collected from the dry Pacific forest at Jaco, Costa Rica, to provide a comparison with the La Selva genotype. Germinating seeds were sown in a 1:1 mixture of old alluvial soil and river sand in pots of 10 cm diameter that were 75 cm or more deep. Seeds were considered germinating if the radicle had emerged. Germinating seeds were obtained from seeds germinated in flats or from seeds collected directly from the forest floor. Seedlings were grown in a shadehouse in which daily irradiance determined by a quantum integrator averaged 36 to 38% of full sun. Soil moisture was maintained at or near field capacity by a combination of natural rainfall and supplementation by well water.

After one and two months growth, containers were carefully dismantled and the seedlings of each species were measured for depth of longest root and leaf area. Plants were separated into leaves, stems, and roots, dried for 48 hours at 70 ^{o}C, and weighed. Harvest data were used for calculation of relative growth rate over the interval between the months one and two. Sample sizes were from five to ten plants per harvest. For seed dry weight values, the dry weight (80 ^{o}C) of 10 or more seeds was measured for all species except for *Pterocarpus haysii* (N = 3).

Both the mean maximum root depth and the maximum root depth observed for a species were not significantly correlated with mean seed weight as tested by Spearman Rank Correlation on log-transformed data (Table 1); the correlation was stronger after two months of growth than after one month. The maximum observed root depth for a species was very poorly correlated with mean seed weight after one month and even less after two months. As might be expected, total plant weight and leaf area were positively correlated with seed weight. Analysis of variance of the log-transformed root depths revealed a significant species effect ($P < 0.0001$), but the maximum root depths of some of the small-seeded species were not significantly different from those of the large-seeded species (Table 2). Thus, despite having total plant weights one-tenth or less than those of the large-seeded species, seedlings of small-seeded species produced comparable root depths.

This rapid production of deep roots by species with small seeds can be attributed in part to their high growth rates which compensate for the lack of stored reserves. Species with small seeds had higher growth rates than species with large seeds as indicated by a significantly negative correlation between relative growth rate and seed weight (Table 1). A similar correlation between seed size and growth rate has also been reported for 24 species of Compositae by Fenner (1983). The high growth potential results in part from greater allocation of biomass to leaf area for small-seeded species than for large-seeded species. Both the leaf area ratio (ratio of total leaf area to total plant weight) and specific leaf area (ratio of leaf area to leaf weight) were greatest for species with the smallest seeds (Table 1). Species differences in relative growth rate in the present study would have been even greater under higher growth irradiances such as those of large clearings where seedlings of small-seeded species are usually found; at 38% of full sun, the small-seeded pioneer species are likely to be light limited whereas the large-seeded shade-tolerant species are not (Bazzaz & Pickett 1980).

TABLE 1

*Spearman Rank Correlation (r_S) between log-transformed seed weight and log-transformed root and growth characteristics. Symbol: *, significant at $P < 0.05$*

Characteristic	r_S
Mean maximum root depth (1 month)	0.21
Mean maximum root depth (2 months)	0.48
Maximum observed root depth (1 month)	0.15
Maximim observed root depth (2 months)	0.04
Relative growth rate	-0.73*
Total plant weight	0.79*
Total leaf area	0.68*
Specific leaf area	-0.78*
Leaf area ratio	-0.94*
Root to shoot ratio	0.09

The species tested also differed in root morphology. The small-seeded species tended to have finer roots than the large-seeded species as indicated by their greater root length per unit root weight (Table 2). As a result, comparable root depths were attained by small-seeded species with lower investment in biomass. Furthermore, differences in allocation patterns may favor root growth or depth regardless of seed size, as can be seen by the lack of a correlation between root to shoot ratios and seed weight. For example, although the differences were not significant, of the two genotypes of *O. lagopus*, the genotype from the dry site had the deepest roots even though it had smaller seeds.

TABLE 2

Mean maximum root depth and biomass characteristics of tropical tree seedlings one and two months after germination. Means of root depth with different letters are significantly different at the 5% level as tested by one way analysis of variance and Fischer's least significant difference test on log-transformed data

Species	N	Seed weight (g)	1 month root depth (cm)	2 months root depth (cm)	Length to weight ratio ($m\ g^{-1}$)	Total plant weight (g)	Leaf area (cm^2)
Heliocarpus appendiculatus Turcs.	5	0.0005	16.7 bcd	26.0 bcd	8.0	0.26	61.2
Ochroma lagopus Swartz (Jaco)	6	0.0068	25.2 a	37.9 abc	24.6	0.07	13.5
Ochroma lagopus Swartz (La Selva)	8	0.0071	19.3 abc	34.6 abc	18.0	0.06	13.2
Cordia alliodora (R.&P.) Oken	10	0.0081	13.1 cd	19.6 cd	8.7	0.08	16.6
Cedrela mexicana Roem.	7	0.0095	12.1 cd	20.3 cd	4.7	0.12	17.7
Stryphnodendron excelsum Harms	8	0.0649	13.6 d	35.4 abc	5.2	0.22	42.5
Bursera simaruba (L.) Sarg.	6	0.0994	12.3 cd	39.7 a	2.2	0.80	117.6
Pterocarpus haysii Hemsl.	6	0.1900	23.8 ab	29.8 bcd	2.4	0.37	31.7
Dipteryx panamensis (Pitt.) Record	6	1.8669	25.4 a	36.6 abc	0.5	2.56	335.8
Pentaclethra macroloba (Willd.) Kuntze	6	4.2670	22.2 abc	42.6 a	0.5	3.47	274.9

Seed size is subject to a variety of post-dispersal selective pressures. Putz (1983) suggested that small-seeded species would have difficulty pushing radicles through litter. However, large seeds may germinate more slowly than small seeds because larger seeds make poorer contact with the germination substrate. Swamp species often have very large seeds, presumably to rapidly produce shoots that will extend above the water level (McHargue & Hartshorn 1983). As a result of sometimes opposing selective pressures, seed size is not necessarily a good predictor of the belowground performance of seedlings of different species.

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