GROWTH RESPONSE OF *Cecropia obtusifolia* TO GREENHOUSE FERTILIZATION[1] /

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Resumen

El crecimiento de plántulas de Cecropia obtusifolia *bajo nueve niveles de fertilización fue estudiado en un invernadero en Washington, EE.UU. Después de ocho meses, la biomasa total fue mayor en los tratamientos con calcio (más otros elementos) y menor en los tratamientos sin nitrógeno y/o fósforo. Las concentraciones de N, P y K fueron más altas en el follaje nuevo que en el follaje viejo. Se discuten posibles adaptaciones de* Cecropia *que podrían favorecer su establecimiento en áreas de crecimiento secundario, tales como la eficiencia en la absorción de nutrimentos o la capacidad para redistribuir nutrimentos dentro de la planta misma.*

Introduction

Cecropia obtusifolia Bertol. is a fast-growing tree species characteristic of disturbed sites in many lowland forests of tropical America. The early colonization and rapid growth of pioneer species, such as *Cecropia*, has been suggested as a means by which second-growth ecosystems recover and immobilize nutrients that would otherwise have been lost (1, 9, 11). This assumes that there is a greater possibility of nutrient loss from ecosystems at times of increased nutrient availability (e.g. after a burn or after fertilization) and that second-growth ecosystems respond to increased nutrient availability by accumulating more biomass. This, however, did not occur in a fertilization study by Harcombe (7). Harcombe showed that biomass production in a Costa Rican forest ecosystem was not stimulated by fertilization; rather, fertilization promoted the growth of forbs, which suppressed shrub and tree growth (one of which was *C. obtusifolia*), and resulted in a lower biomass and nutrient standing crop. In fact, the more rapid growth of *Cecropia* in the absence of surplus nutrients suggested that *C. obtusifolia* may be more competitive on less fertile than on fertile sites. On second-growth sites where *C. obtusifolia* does immobilize relatively large amounts of nutrients, nutrient immobilization through rapid growth seems to be more a consequence of an autoecological adaptation to establishment in disturbed areas (4), rather than the initiation of a "strategy" for ecosystem development. The mechanisms involved in the rapid growth adaptation of *Cecropia* species may relate to an efficient uptake of nutrients on nutrient-poor soils (6) or to inherently low requirements for certain critical elements (8).

In addition to nutrient uptake and requirement mechanisms, another means by which plants can conserve certain nutrients (especially nitrogen) is the redistribution of elements from senescing foliage to younger and actively growing plant parts. Although species vary considerably in their capabilities to redistribute nutrients from senescing foliage, deciduous species (including deciduous conifers) seem to redistribute more nutrients than do evergreen conifers (2).

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The importance of redistribution as a nutrient conservation mechanism for *C. obtusifolia* (a tropical evergreen) is unknown, but the good growth of this species on seemingly infertile soils may in part be sustained by a high degree of nutrient redistribution from senescing foliage.

This greenhouse study was designed to provide preliminary information on the nutrient requirements of *C. obtusifolia* and to examine any effect fertilization may have on nutrient redistribution within the plant.

Materials and methods

The growing medium for the *Cecropia* seedlings was a well-mixed and homogeneous topsoil (Everett series) from the Cedar River watershed of the Cascade mountains, Washington, U.S.A. Topsoil analyses showed the following: 0.15% total nitrogen, 39% base saturation, and 0.25, 1.88 and 2.10 M eq per 100 g for potassium, calcium and magnesium respectively (3). Nitrogen, phosphorus and calcium were relatively low in this soil.

On November 15, 1975, seed was collected from a single *C. obtusifolia* tree near the Organization for Tropical Studies Research Station at La Selva, Costa Rica. Seed from one tree was collected to provide as uniform genetic material as possible. The La Selva research station has been described elsewhere (5). In January, 1976 these seeds were sown on silica sand in the University of Washington greenhouse and were periodically watered with distilled water. On April 21, twenty-eight *Cecropia* seedlings of subjectively equal size and vigor were each transplanted into plastic pots. Pots were approximately 15 cm high and 15 cm in diameter at the top, tapering to 11 cm in diameter at the base. Each pot was filled with approximately 3 000 g (air dry weight) of soil medium. On June 4, after allowing six weeks for seedlings to adjust to the soil, nine treatments were established. There was one control treatment and eight fertilizer treatments (Table 1). Five of the fertilizer treatments had four replications and three of the fertilizer treatments plus the control had two replications. Nitrogen, phosphorus and potassium subscripts on Table 1 indicate hundreds of pounds per acre (89 kg/ha) of a particular element. Treatments receiving lime each had 3.2 g $CaCO_3$ sprinkled on the pot soil. Magnesium treatments each received 0.4 mg MgCl and the boron treatment received 2.8 mg boron. With the exception of lime, all elements were applied in aqueous solutions.

After fertilization (June 4) pots were watered to field capacity twice weekly for eighty-one days. On August 24 all plants were harvested and oven dried for 72 hours at 70°C. Initial (June 4) and final (August 24) height measurements were taken. After harvest, oven dry weights of shoots and roots were determined for each plant.

Table 1. Summary of significant differences among treatments in height increment and biomass production for 8-month old *Cecropia obtusifolia* seedlings. For each column, the appearance of two identical letters denotes a treatment mean that is significantly higher (5% level) than the mean of treatments followed by only one of that same letter.

Treatments*	No. of Replicates	Biomass Total	Biomass Above ground	Biomass Below ground	Height
$N_3P_8K_1$ Mg Lime	4	a a	a a	a a	
$N_3P_8K_1$ Lime	4			b b	
$N_3P_8K_1$ B Lime	4	b b	b b		a a
$N_3P_8K_0$	2	c c	c c	c c	a
$N_3P_8K_1$	4		a		a
$N_3P_8K_1$ Mg	4				a
$N_0P_0K_0$	2	a	a	a b c	a
$N_0P_8K_1$	2	a b c	a b c	a b c	a
$N_3P_0K_1$	2	a b c	a b c	a b c	a

* Nitrogen, phosphorus and potassium subscripts indicate hundreds of pounds per acre (89 kg/ha) of a particular element.

The two uppermost and two lowest leaves of each plant were collected for chemical analyses. Within treatments upper leaves of two plants were combined and lower leaves of two plants were combined to produce an analysis pair. Treatments with four replicates yielded two analysis pairs; treatments with two replicates, only one. In total, 14 analysis pairs of upper and lower foliage (28 determinations) were each ground in a Wiley mill to pass a 40 mesh screen and were analyzed for N, P and K following Parkinson and Allen (10).

Results

Aboveground biomass, belowground biomass, total biomass and total height increment of all treatments (Figure 1 and Table 1) were each analyzed by Duncan's multiple range test for significant differences. Treatments that produced significantly greater biomass or height increment are indicated on Table 1. Biomass production was less in treatments without nitrogen and/or phosphorus fertilizer and greater in treatments receiving lime plus other elements (Figure 1). The mean height increment of *Cecropia* seedlings eight months of age ranged from a low of 10.8 cm in the N_3 P_0 K_1 treatment to a high of 28.5 cm in the N_3 P_8 K_1 B lime treatment (Figure 2). Height increment of this latter treatment was significantly greater than the increment of six of the remaining treatments (Table 1).

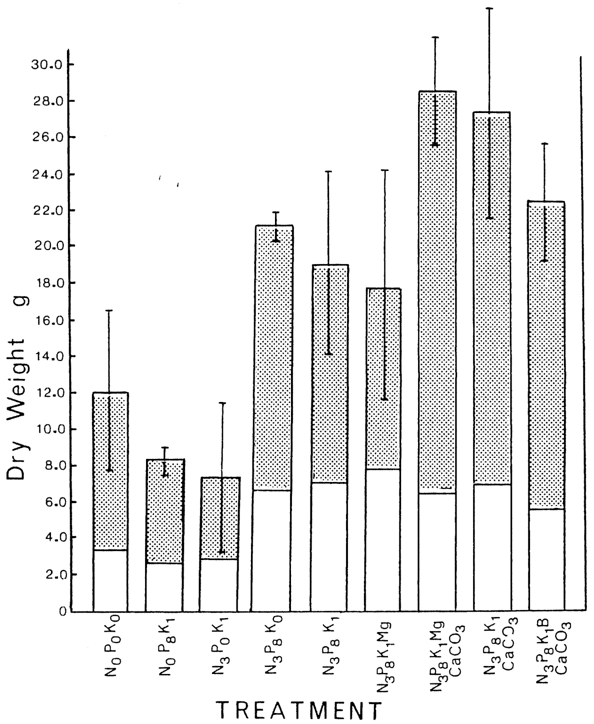

Fig. 1. Total dry weight of eight-month-old *Cecropia obtusifolia* seedlings from nine fertilizer treatments. Clear portions of histograms are below ground biomass. Vertical bars are one standard deviation on both sides of the mean.

To examine fertilizer response and evidence of nutrient redistributions, the concentration of N, P and K in upper relative to lower foliage was examined (Table 2). Nitrogen concentrations in both upper and lower leaves were always less in treatments that did not receive nitrogen fertilizer. Phosphorus concentrations in lower leaves were always less and in upper leaves were nearly always less (one exception) in treatments that did not receive phosphorus fertilizer. Treatments without phosphorus and/or nitrogen fertilizer also had the least total biomass. This suggested that the absence of either nitrogen or phosphorus could limit growth. With only two exceptions, the concentration of N, P, and K in an analysis pair (upper vs. lower leaves) indicated greater nutrient concentrations in upper or younger foliage. This suggested redistribution of nutrients from older to younger plant parts.

Shoot to root ratios (calculated from data in Figure 1) indicated a 2.9 average ratio for the three lime plus other element treatments and a 2.1 average shoot to root ratio for the six treatments without lime. When subjected to a two-tailed t-test, however, this apparent difference was not significant ($P \leqslant 0.05$).

Discussion

The biomass data indicated a response of *C. obtusifolia* seedlings to fertilization. Application of N and P increased seedling biomass, but if either or both of these elements were excluded from a treatment, biomass production was reduced. Of special interest was that among treatments receiving both N and P, the greatest biomass was in treatments receiving lime. Although an influence of other elements was not excluded, this situation suggested a growth response of *Cecropia* seedlings to calcium. This response could be an adaptive mechanism to increase the competitiveness of *Cecropia* on second-growth sites high in calcium. A second mechanism that can help explain the competitiveness of *Cecropia* is the survival of seedlings in treatments without N and/or P. In field conditions N or P availability may continually fluctuate due to input from decomposition, rainfall, etc. Since *Cecropia* seedlings can survive low nutrient conditions for at least 8 months, established plants are available to respond, perhaps more quickly than competitive species, to times of greater nutrient availability. This possible competitive advantage for *Cecropia* seedlings on nutrient-poor soils is substantiated by Harcombe (7) who indicated that when nutrients

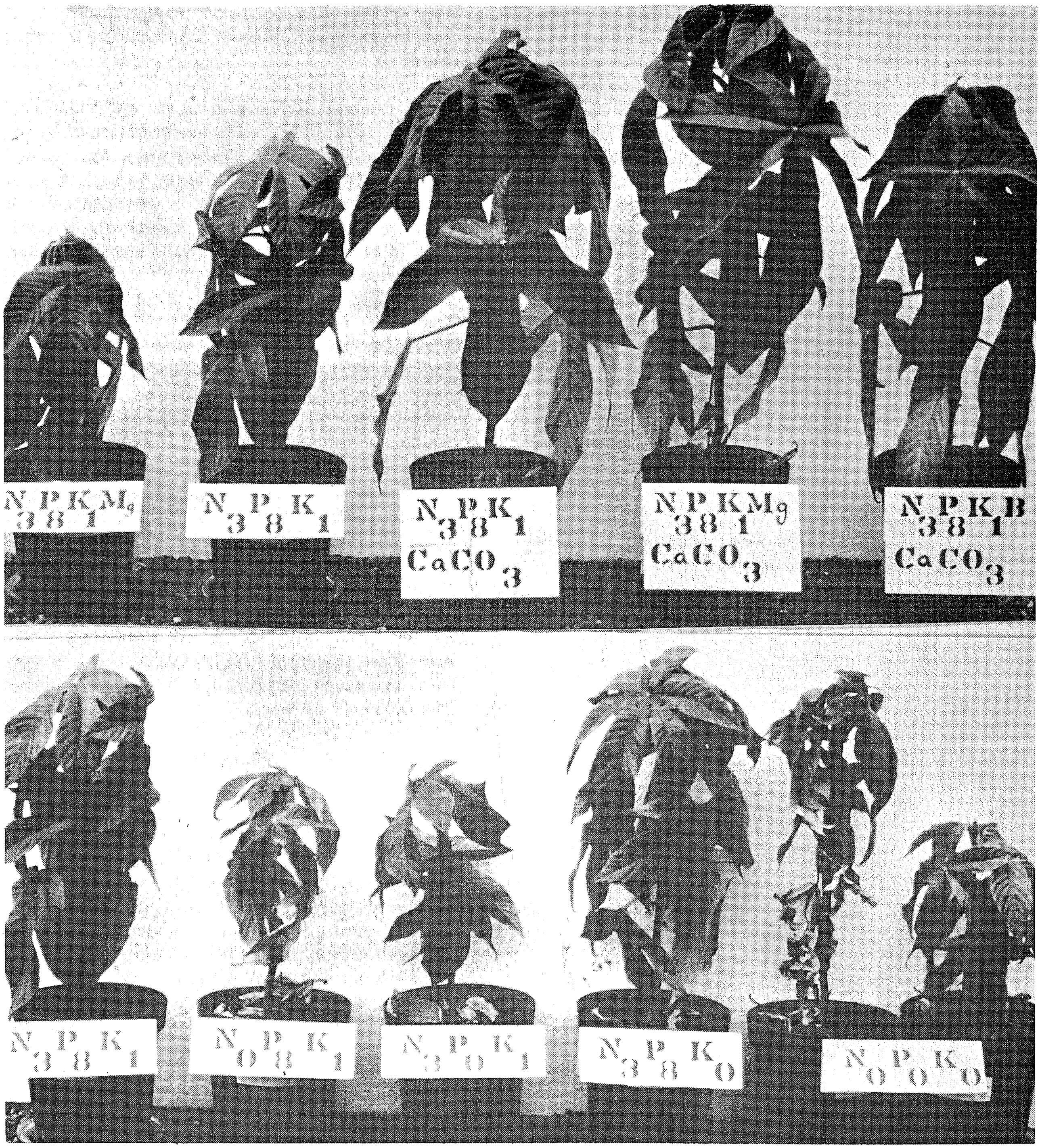

Fig. 2. Appearance of *Cecropia obtusifolia* plants from each fertilizer treatment. Scale: Pot Height = 15 cm.

were made available, the biomass of *Cecropia* was reduced.

The greater concentration of N, P, and K in younger than in older leaves was indirect evidence that redistribution of these elements from senescing to younger foliage had occurred. An alternative, less likely explanation could be that the first formed, lowermost leaves were low in nutrients as juvenile leaves and sustained a low nutrient concentration until senescence. In this greenhouse study there was no leaching by rain of foliar elements, substantiating

Table 2. Concentrations of N, P, and K in the two uppermost and two lowest leaves of greenhouse-grown *Cecropia obtusifolia*.

Treatment	Shoot dry wt (g)	Percent nitrogen		Percent phosphorus		Percent potassium	
		upper	lower	upper	lower	upper	lower
1. *$N_3P_8K_1$ Mg Lime	20.5	2.05	1.84	0.518	0.371	1.26	0.79
2. *$N_3P_8K_1$ Lime	20.4	2.17	1.81	0.638	0.371	1.32	0.80
3. *$N_3P_8K_1$ B Lime	16.7	2.03	1.82	0.684	0.362	1.25	0.72
4. $N_3P_8K_0$	14.7	2.17	1.56	0.421	0.614	1.45	1.63
5. *$N_3P_8K_1$	12.2	2.11	1.98	0.472	0.275	1.62	1.35
6. *$N_3P_8K_1$ Mg	11.4	2.11	1.64	0.480	0.264	1.66	0.94
7. $N_0P_0K_0$	8.5	1.51	1.07	0.355	0.183	1.47	1.16
8. $N_0P_8K_1$	6.0	1.52	1.01	0.204	0.488	0.61	1.13
9. $N_3P_0K_1$	4.7	2.11	1.64	0.295	0.170	1.97	1.21

* Values of these treatments are the mean of two chemical analyses, and the others, only one analysis

the possibility that low nutrient levels in senescing foliage were the result of redistribution to younger plant parts.

The difference in foliar nitrogen levels between upper and lower leaves was similar for nitrogen-fertilized and nitrogen-unfertilized treatments. Since greater redistribution did not occur in treatments without nitrogen, by harvest time plants of all treatments may have been nitrogen deficient. Alternatively, *Cecropia* plants may redistribute similar amounts of foliar nitrogen from senescing foliage in quite different nutrient regimes. Redistribution of foliar elements from senescing foliage suggests a more efficient utilization of these elements. Further data may determine the redistribution patterns in *Cecropia* as different from those in tropical species from later successional stages.

Summary

The growth response of *Cecropia obtusifolia* seedlings at nine fertilization levels was studied in a greenhouse in Washington, USA. After eight months, total biomass was greatest for treatments receiving lime plus other elements and least for treatments without nitrogen and/or phosphorus. Concentrations of N, P and K were greater in younger than in senescing foliage. Adaptations of *Cecropia* relating to nutrient uptake and redistribution within the plant that could contribute to the success of this species in second growth situations are discussed.

Literature cited

1. BUDOWSKI, G. Forest succession in tropical lowlands. Turrialba (Costa Rica) 13(1): 42-44. 1963.

2. COLE, D. Nitrogen uptake and translocation by forest ecosystems. **In** Clark, F. E. y Rosswall, T., eds. Terrestrial nitrogen cycles: processes ecosystem strategies and management impacts. Stockholm, Swedish Natural Science Research Council, 1981. 714 p. (Swedish Natural Science Research Council. Ecological bulletins No. 33).

3. COLE, D. W., GESSEL, S. P. and DICE, S. F. Distribution and cycling of nitrogen, phosphorus, potassium and calcium in a second-growth Douglas-fir ecosystem. **In** Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. University Maine Press, 1967. pp. 197-232.

4. DRURY, W. H. and NISBET, I. C. T. Succession. Journal of the Arnold Arboretum 54:331-368. 1973.

5. FRANKIE, G. W., BAKER, H. G. and OPLER, P. A. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881-919. 1974.

6. GOMEZ–POMPA, A., and VASQUEZ–YANES, C. Studies on the secondary succession of tropical lowlands: The life cycle of secondary species. Proc. First International Congrese Ecology, The Hague 1974. pp. 336-342.

7. HARCOMBE, P. A. The influence of fertilization on some aspects of succession in a humid tropical forest. Ecology 58:1 375-1 383. 1977.

8. KELLMAN, M. C. Some environmental components of shifting cultivation in upland Mindanao. Journal Tropical Geography 28:40-56. 1969.

9. MARKS, P. L., BORMANN, F. H. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science 176:914-915. 1972.

10. PARKINSON, J. A. and S. E. ALLEN. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Comunications Soil Science and Plant Analysis 6(1): 1-11. 1975.

11. VAN STENNIS, C. G. G. J. Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. **In** Study of Tropical Vegetation. Paris, UNESCO, 1958. pp. 212-218