Regeneration and Growth Strategies of *Brosimum alicastrum* Sw. in the Moist Tropical Forests of Mexico

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Introduction

Brosimum alicastrum (Moraceae) is a large evergreen tree which is widely distributed throughout Mexico and Central America. The species possesses edible fruits (Figure 1); its seeds are exceptionally rich in protein, its leaves provide a palatable forage, its wood is excellent for construction, and several parts of the tree have medicinal properties. The tree is also known to occur naturally in nearly pure stands in the northern part of its range. This multi-purpose tropical forest species represents a virtually untapped source of food and forage. The utilization of natural forests of the tree would increase significantly the amount of quality protein available to rural populations in the moist tropics, while the establishment of forage plantations would provide an alternative to the continued conversion of tropical forest to pasture. The development of *B. alicastrum* as a resource, however, has been severely limited by a lack of basic information about the ecology of the species.

Objectives

To:

- characterize the structure and distribution of an undisturbed, high density forest of the species;
- quantify size-specific flower and fruit production;
- document the ecological factors which control seedling establishment and growth; and
- construct a predictive model of the regeneration and growth of the species to assess the impact of seed collections on the long-term stability of the forest and to serve as a guide in the development of management plans.

FIGURE 1. Fruiting branch of *B. alicastrum*.

Approach

A three-year study of the establishment, growth and reproduction of *B. alicastrum* in Mexico was designed in cooperation with the Instituto Nacional de Investigaciones sobre Recursos Bióticos (INIREB) of Xalapa, Veracruz. The basic focus of the study was that of plant demography, i.e., the repeated observation and measurement of marked individuals within a permanent study site. A tract of semi-evergreen forest containing a high density of *B. alicastrum* was selected for study near the town of Papantla in northern Veracruz. A series of contiguous lots representing a total area of one hectare was established within the forest, and all *B. alicastrum* individuals in each plot were measured for height and diameter, plotted on a grid map, and permanently numbered with a metal tag (Figure 2). Canopy gaps, treefalls, and stumps were also mapped, and seedling inventories were stratified by canopy cover. The growth, survival and reproduction of each marked individual was monitored biweekly over a period of three years. The growth in height of seedlings and saplings was measured directly, while vernier-type dendrometer bands were used to record the diameter increment of larger individuals.

Size-specific flower and fruit production was measured over two fruiting seasons by locating

FIGURE 2. Profile diagram of a 20 × 50 meter transect of *B. alicastrum* forest near Papantla, Veracruz, Mexico. *B. alicastrum* trees are shown with shaded crowns. Associated species include MZ (*Manilkara zapota*), MM (*Mirandaceltis monoica*), TJ (*Trichilia japurensis*), GA (*Guatteria amplifolia*), and RG (*Rinorea guatemalensis*). Note steep slope and imbrication of tree crowns.

litter traps under the crowns of reproductive individuals of differing size. Pollination, fruit maturation and dispersal were studied in greater detail through the use of special tree climbing equipment (Figure 3).

The effect of light level on seedling growth and photosynthesis was examined in a series of laboratory and greenhouse experiments. Seeds from the study area which had been stratified by size were germinated and then transplanted in a greenhouse where they were maintained under three different light environments (2%, 48%, and 100% full sun). The height and leaf area of the seedlings in each treatment were recorded weekly for six months and the photosynthetic response of a subset of seedlings was also measured. Seedling photosynthesis was determined using an open gas-exchange system which provided precise control of leaf temperature, light level, flow rate and gas concentration in the airstream.

Major Findings

The laboratory and field experiments revealed that treefall gaps play an important role in the regeneration strategy of *B. alicastrum*. Differential mortality was found to be responsible for the observed aggregation of seedlings along the perimeter of canopy gaps and for 50-70% of all saplings and juveniles being located within four meters of an old treefall.

The photosynthetic response of *B. alicastrum* seedlings provides a physiological explanation for the enhanced establishment observed around canopy gaps. Light levels along the edge of canopy gaps allow *B. alicastrum* seedlings to express their maximum photosynthetic potential. Seedlings which become established in this microenvironment, therefore, have a competitive advantage over those growing under other types of canopy cover.

FIGURE 3. Tree climbing in floral biology studies of *B. alicastrum*.

Flowering and fruiting in *B. alicastrum* is also unique (Figure 4). The population is gynodioecious, i.e., with female and hermaphroditic trees, and pollination is primarily by wind. Flower production peaks during the February-March dry season, with mature fruit falling during the onset of the summer rains in May-June. A large percentage (60-70%) of the flowers produced by female trees are pollinated and form fruit, and fruit production increases with tree size up to a maximum of 65 kilograms per tree. Pollination efficiency and fruit production for hermaphroditic trees, on the other hand, are much less, and decrease consistent with tree size to the point that the largest individuals in the population produce no fruit and are functionally male. All small trees are females, intermediate size trees are hermaphrodites, and the largest trees are male. This distribution coupled with the flower and fruit production data seems to suggest that *B. alicastrum* is a sequential hermaphrodite, i.e., that individual trees pass through female, hermaphrodite and male sexual states during their development. In essence, the tree changes sex as it moves upward through the canopy.

Two developmental pathways seem to be available, however, because a few large females were found in the population. After an individual reaches 10-15 centimeters in diameter, it begins to produce female flowers and form fruit. If the tree happens to be growing under a relatively open canopy, it will retain its female sexual expression as it increases in diameter. Female trees which are growing under suppressed conditions, however, gradually initiate the production of male flowers, and hence, become functionally hermaphroditic. This change in sexual expression seems to occur at approximately 25 centimeters in diameter. With further increases in diameter, female flower production is gradually eliminated and the tree begins to function solely as a pollen donor.

The plastic sexual expression exhibited by *B. alicastrum* seems to represent a reallocation of resources from reproductive functions to vegetative growth. As the energetic costs of producing pollen are much less than that required for maturing a large crop of protein-rich seeds, a hermaphrodite or male tree would seem to have a greater survival probability in a resource limited environment. In addition, considering that the species is pollinated by wind, tall males and short females make good biological sense.

A final result of importance from the ecological study of *B. alicastrum* is that the high-density population near Papantla was found to be a stable and self-maintaining aggregation. Based on the detailed demographic data which was collected, mortality was shown to be balanced almost exactly

FIGURE 4. Mature and developing fruit, hermaphroditic flowers and seed of *B. alicastrum*.

by the recruitment of new seedlings. In addition, computer simulations indicated that intensive seed collections would have little effect on the long-term stability of the forest, even if conducted on an annual basis. Natural forests of the species, therefore, are stable, highly productive systems which can be exploited on a sustained basis with a minimum of ecological impact.

Implications

The research has illuminated the potential of *B. alicastrum* to improve the food production capabilities and welfare of rural populations, and has expanded current knowledge of the structure and function of tropical moist forests. The results from this work provide a scientific basis for the management of natural forests or plantations of *B. alicastrum*, and underscore the value of doing cooperative research at an international level.

Policy and Management Guidelines

Plantation efforts should be concentrated on the production of forage rather than fruits as a result of the labile sexuality of the species, e.g., a pollen source would be lacking in even-aged systems.

In forage plantations the species should be interplanted under fast-growing legume trees, due to its ability to withstand partial shade.

The use and conservation of natural forests of the species should be promoted as sources of high quality protein to be used either for human consumption or as livestock feed.