

Growth Rates of *Welfia georgii*, *Socratea durissima*, and *Iriartea gigantea* Under Various Conditions in a Natural Rainforest in Costa Rica

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The abundance and diversity of subcanopy palms lends a characteristic appearance to most neotropical wet forests. From small shrubs to large understory trees, the palm family is one of the most common and obvious features of these forests. Since palms are so abundant, their influence on the total dynamics of the forest is likely to be significant. Although considerable effort has been expended on other aspects of palms, they have been little studied in their natural environment from an ecological point of view. For example, in Corner's natural history (1966), not one of the 15 chapters is devoted to palm ecology. Notable exceptions are Michalowski's (1958) short discussion of the ecology of Paraguayan palms, Bannister's study of *Euterpe globosa* [= *Prestoea montana*] (1970), Kiew's (1972) notes on *Iguanura*, some recent pollination work (Schmid, 1970, 1970a; Essig, 1971, 1973), and work on seed predation (Janzen, 1971, 1972; Wilson and Janzen, 1972).

The theoretical impetus for the present study comes from a well known pattern of forest dynamics. As articulated by earlier authors (e.g. Jones, 1945; Watt, 1947) and somewhat modified recently (e.g., Gomez-Pompa, *et al.*, 1972; Horn,

1974), patterns of light interception in a forest result from the process of old trees falling and the resulting light gap gradually returning to the original state through the process of ecological succession. Thus, at a given time, a forest is expected to contain patches of light (light gaps) of various ages and origins, some recently created by a falling tree and therefore open almost completely to the sky and others created long ago, virtually filled with old vegetation and therefore relatively dark in the understory. The various types of light gaps found in a primary forest provide a variety of special habitats for any plant species. In an attempt to understand how some common understory palms fit into this general picture, data were obtained for *Welfia georgii*, *Socratea durissima*, and *Iriartea gigantea* with regard to relative growth rates under different light conditions.

All three species are common in the Atlantic lowland of Costa Rica, principally as subcanopy trees; however, *I. gigantea* and *S. durissima* frequently reach the main canopy and may even emerge. These three palm species have no economic importance, but we suspect that their impact on the total dynamics of the forest is great.



1. A light gap in the forest at La Selva, Costa Rica. Left, typical canopy cover above a minor light gap; Right, understory in the same light gap.

Methods

The study was undertaken at the La Selva field station, owned and operated by the Organization for Tropical Studies, in the Atlantic lowlands of Costa Rica. The site is located in neotropical lowland wet forest (Holdridge, 1967) and has particularly abundant populations of the three species in question. The site is characterized by a complicated pattern of old and new alluvial deposits along with extensive residual soils and is interrupted by many swamps and streams. These topographical factors result in high habitat diversity. In an attempt to sample from a variety of habitats, plants were selected from five different areas.

The sampling procedure involved first, classification of the habitat and second, measurement of relative growth rate of the individual.

The habitat classification was made for each individual plant by examining qualitatively the situation in which the plant was found, and placing it into one of the following categories:

- (1) "Climax"—complete canopy cover, dark understory.
- (2) Major light gap, not overtopped—relatively recent large treefall such that any plant in the area was more or less completely exposed to open sky.
- (3) Major light gap, overtopped—same as (2) except the plant in question was overtopped by a vine or other second growth species.
- (4) Minor light gap—reasonably complete canopy cover, but a paucity of understory trees such that a medium amount of light was falling to the forest floor due to diffuse light coming through the relatively thin upper canopy (see Fig. 1).

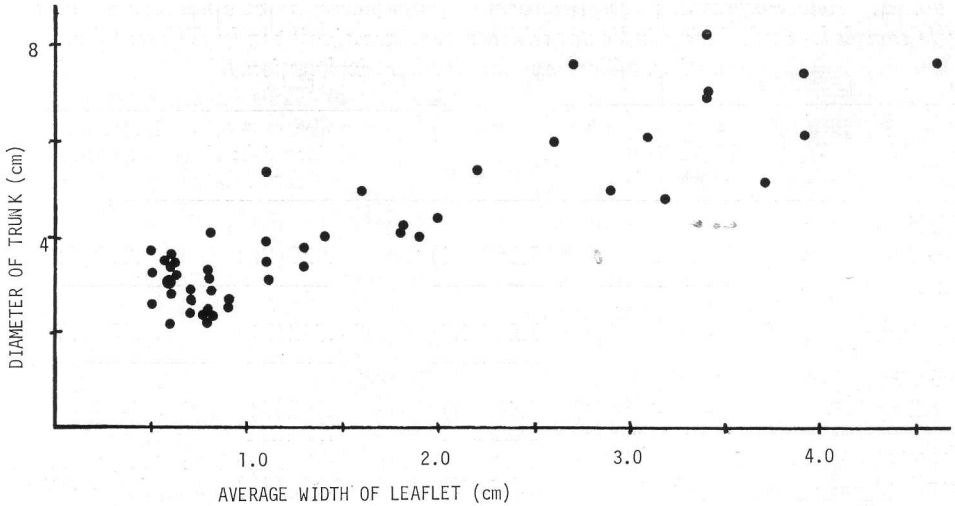
The above categories were defined qualitatively owing to the lack of any kind of sophisticated apparatus to measure continuously the pattern of light interception in the forest. In a large proportion of samples (depending on the area, perhaps up to 50 percent), it was impossible to classify the state of the forest. Any plant occurring in such a sample was omitted from the analysis; only those plants which clearly fell into one of the four categories were considered.



2. *Weljia georgii* at La Selva, Costa Rica. a, closeup of a seedling; b, a small sapling; c, a large sapling; d, an adult; e, closeup of *Weljia* infructescences. Note inflorescence at left with male flowers.

Our method of estimating the relative growth rates of individuals rests on a knowledge of the developmental morphology of the palm leaf. Consider the growth pattern of *Weljia*. Upon ger-

mination, one leaf bearing two leaflets is sent up. The next few leaves each have two leaflets. After a certain number of leaves have been produced the succeeding leaves have more than two leaflets.



3. Diameter of trunk as a function of average width of leaflet for seedlings of *Welfia*.

Under favorable light conditions, each of these new leaves will have more leaflets than the previous one. This process continues until the tree begins growing upward. It then grows to a height of six to twenty meters at which point it begins fruiting. This pattern of growth is common for many palms (Tomlinson, 1960, 1961; Kiew, 1972). We have classified all individuals into seedling or sapling, based on this developmental sequence. A seedling is defined as any plant whose leaves contained only two leaflets. Any individual *Welfia* that had at least one leaf with more than two leaflets and that exhibited no above ground stem (trunk) was considered a sapling (Fig. 2b, c). Individuals of *Iriartea* and *Socratea* were considered saplings if they had at least one leaf that had more than two leaflets and if the growing tip was no higher than six feet above the ground.

During the seedling and sapling stages of *Welfia* the trunk, which is beneath the ground, increases in diameter up to a critical point at which time the tree begins growing upward (Tomlinson, 1960). In order to categorize individual seed-

lings and measure their growth rate, it was necessary to find some above ground characteristic which correlates with the trunk diameter. A sample of fifty seedlings of various sizes was collected, several leaf characteristics measured on each leaf, and the diameter of the trunk measured. Of the characteristics measured, the average width of the two leaflets appeared to show the highest correlation with trunk diameter. This relationship is shown in Figure 3. Clearly, as leaf width increases, the diameter of the trunk increases and, therefore, the relative growth of an individual plant can be estimated by the increment of leaflet width of successive leaves.

Although the early growth of stilt root palms such as *Socratea* and *Iriartea* is basically different from that of *Welfia* (Tomlinson, 1960), this difference has no important consequences for the implications of this study. Therefore, we presume that the growth rate of seedlings of all three species can be estimated by the increment of leaflet widths.

Reasoning simply from the developmental morphology of the leaf of these

Table 1. Relative growth rates. Numbers in parentheses indicate number of individuals sampled. Underlining indicates which means are significantly different from one another. (See text for further explanation.)

	Major light gap (overtopped)	"Climax"	Minor light gap	Major light gap (not overtopped)
<i>Welfia</i> seedlings	<u>1.087(8)</u>	<u>1.168(44)</u>	<u>.929(22)</u>	<u>.872(6)</u>
<i>Welfia</i> saplings	—	<u>1.203(27)</u>	<u>.842(21)</u>	<u>.830(9)</u>
<i>Iriartea</i> seedlings	—	<u>1.405(8)</u>	<u>.891(4)</u>	—
<i>Iriartea</i> saplings	—	<u>.892(7)</u>	<u>.893(13)</u>	—
<i>Socratea</i> seedlings	—	<u>1.175(12)</u>	<u>.856(11)</u>	—
<i>Socratea</i> saplings	—	<u>.836(6)</u>	<u>.811(5)</u>	—

three species, it is obvious that relative growth rates of saplings can be estimated by the increment in leaflet numbers of successive leaves.

Thus we have methods for estimating growth rates of both individual seedlings and individual saplings. Obviously these techniques do not permit us to say anything about absolute growth rates since the rate of actual leaf development and senescence is not actually known and is probably not even approximately the same under different conditions (Smith, 1963). However, they are certainly reasonable techniques for looking at the population from a qualitative point of view.

Results and Discussion

Considering only the youngest and next youngest leaf, we can compute the ratio between the two (leaflet widths for seedlings and leaflet numbers for sap-

lings), taking the youngest leaf as the denominator. Thus, if we have a ratio greater than 1, the plant may be said to be declining, whereas a ratio less than 1 indicates that the plant is growing. The combined data for all five sampling areas and computations of the mean ratio for each canopy type for each of the three species are presented in Table 1. Duncan's Multiple Comparisons test was used for the *Welfia* data and a standard student's t-test was used for the *Iriartea* and *Socratea* data. The underlined values in Table 1 indicate the level of statistical significance. Two means that are connected by underlining do not differ from one another but do differ from any mean that is not connected to them through underlining. Thus, for example, the growth of *Welfia* seedlings in minor light gaps (.929) is not significantly different from growth in major light gaps when they are not over-

topped (.872); however both of these means are significantly different from both growth in a climax area (1.168) and growth in major light gaps if they are overtopped (1.087). Similarly, the growth of *Iriartea* seedlings in a climax situation is significantly different from growth in a minor light gap; whereas, the growth of *Iriartea* saplings in a climax area is not significantly different from growth in a minor light gap.

Consider first the data on *Welfia*. In a climax situation *Welfia* exhibits a declining growth rate (1.168 for seedlings and 1.203 for saplings). This growth pattern is not significantly different from that of individuals overtopped in a major light gap. However, in either a minor light gap or a major light gap when not overtopped, both seedlings and saplings exhibit positive growth rates. Thus, it would appear that *Welfia* is a "specialist" on a certain type of light gap, i.e., what we are here calling a minor light gap. *Welfia* seedlings and saplings are not able to grow in a perfectly climax situation and lose out in biological competition with other second growth species in a major light gap situation.

The data for *Iriartea* and *Socratea* are somewhat scanty; however, the trend seems to be similar to that of *Welfia*. Both *Iriartea* and *Socratea* show the same pattern as *Welfia* for climax areas and minor light gaps in the seedling stage. However, in both genera the saplings do not seem to show this trend. Once *Iriartea* and *Socratea* reach the sapling stage, they apparently are capable of growth even under climax situations. It is tempting to look at differences in the actual values of these ratios between species and between seedlings and saplings; however, this is most certainly not valid because for all cases, different life forms are represented and

the ratios therefore are in no way comparable. The data are useful only to look at relative growth rates of the same life form under different environmental conditions.

In view of the above results, it would appear that the pattern of light interception in the forest is extremely important to the population dynamics of all three species. It appears that these three species are similar qualitatively in that, in the climax forest after seed dispersal by birds or mammals, the seedling exists very near or below its compensation point. That is, each leaf photosynthesizes just enough to produce another leaf of the same size and morphology. In fact it seems that in a truly climax situation the seedling is actually below its compensation point. In the absence of a tree-fall in the near vicinity, the seedling will eventually die. If a treefall does occur, the seedling immediately begins growing and continues to do so until the light gap is grown over. However, if the treefall is very close to the seedling, or for some other reason the resultant light gap is very large, vines and other rapidly growing second growth species choke out the seedling. Thus, the three palm species are specialists on a particular type of light gap. If the gap is too small the plant remains near or below its compensation point and eventually dies. If the light gap is too large, other species competitively drive the plant to extinction.

This dynamic situation points to a rather interesting interrelationship between a population and the environment in which it exists, possibly a very general interrelationship which might be incorporated into a more abstract theoretical framework. These three palms respond to particular patterns of light interception in the forest, but, owing to their abundance, they are strongly implicated in causing these particular patterns.

Thus the physical environment (light patterns) dictates the mode of growth and survival of these populations, and these populations (*Welfia*, *Socratea*, *Iriartea*) dictate the mode of formation of patterns of light interception (the physical environment). Thus, we have a cyclic process where physical factors are determined by biological factors, and vice versa.

The rather gross qualitative way in which these data were collected is sufficient to demonstrate the point of the paper, but not sufficient to gain quantitative information such that a mathematical model of the effect on the population dynamics can be constructed. Clearly, what is needed is some way of measuring the light conditions in specific areas and correlating those light conditions with growth and survivorship properties of individual plants at different life stages. If these measurements could then be tied to the development of the forest in general, one could make predictions about the future history of any one of these populations under various types of forest modification.

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