Principes, 30(3), 1986, pp. 105–107

Plant Architecture and Population Ecology in the Palms Socratea durissima and Scheelea zonensis on Barro Colorado Island, Panama

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In recent years there has been considerable interest in the great diversity of architectural forms in tropical trees. In an effort to investigate the ecological significance of plant forms, studies of plant architecture, photosynthetic responses, and population biology were carried out on the palms *Socratea durissima* and *Scheelea zonensis* (Fig. 1) on Barro Colorado Island from 1981 to 1985.

The growth forms of the palm species *Socratea durissima* and *Scheelea zonensis* were analyzed as a test of the hypothesis that plants show patterns of biomass allocation and canopy architecture that can be used to explain their light requirements, and that differences in architecture between species will lead to predictable consequences at the population level. Results are summarized in Table 1 and are discussed below.

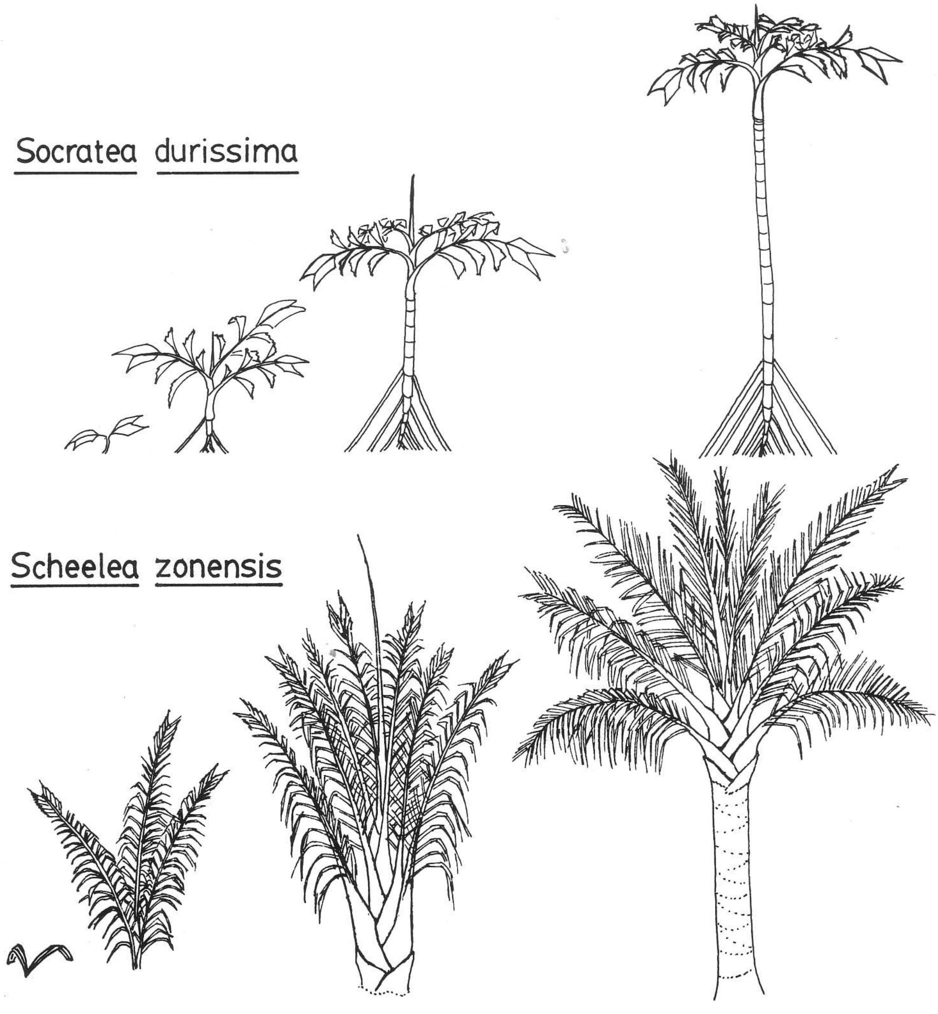
Scheelea allocates more biomass to leaves as a juvenile than *Socratea* does, which may result in a relatively lower respiratory load and allow the light-demanding *Scheelea* to persist in the understory. However, as *Scheelea* grows it accumulates non-photosynthetic biomass and self-shading increases. These factors in combination probably cause the light requirements of whole plants to increase significantly as they mature.

Socratea, in contrast, has a canopy architecture that produces a horizontally oriented leaf display with relatively little self-shading. This species allocates biomass to stem tissue even as a seedling, which could reduce its shade tolerance, but elevating the leaf display may in the long run be beneficial, especially where vertical gradients of light are steep.

Integrated measurements of light levels indicate that light attenuation with increasing depth in the canopy of an individual plant is greater in *Scheelea* than in *Socratea*.

Photosynthetic responses to variation in the light environment enhance the effects of architectural differences. Photosynthesis is better adapted to low light in *Socratea* than in *Scheelea*. Photosynthetic responses in *Scheelea* show a greater ability to acclimatize to high-light environments.

The above results have established that 1) the two species differ in their architecture, 2) the differences in architecture have a significant effect on the distribution of light within the canopies of individual plants, and 3) differences in light requirements resulting from the differences in architecture are enhanced by the differences in photosynthetic responses to light intensity. In order to establish that plant architecture has significant consequences for the ecology of these species, it is necessary to show that growth-rate responses to light differ between species in the man-



1. Developmental stages of the study species.

ner one would predict from the architectural differences. For this purpose plants in natural populations and seedlings in experimental gardens were used to assess the effect of canopy openness on plant growth rates and leaf demography. *Socratea* is better able to grow under low light than is *Scheelea*, but leaf survivorship is lower in *Socratea*. Growth in *Scheelea* shows a greater response to increased canopy openness than in *Socratea*. Average growth rates for size-classes and the degree of canopy openness above individual plants of each species suggest that *Socratea* may be able to attain maturity under relatively closed forest conditions, while *Scheelea* on average is growing slowly or actually declining, suggesting that it may require a large gap in the canopy in order to grow to maturity. Higher rates of leaf turnover in *Socratea* are in contradiction with expectations for sun vs. shade plants, but

Table 1. Summary of architectural, photosynthetic, and population-level differences between Socratea durissima *and* Scheelea zonensis *on Barro Colorado Island, Panama.*

Character	*Socratea*	*Scheelea*
Seed dormancy	no	yes
Percent total biomass in leaves	low	high
Leaf overlap	low	high
Leaf angles	more horizontal	less horizontal
Light attenuation in individual canopies	low	high
Photosynthetic responses	shade-adapted	less shade-adapted
Photosynthetic acclimation to high light	lower	higher
Vertical growth	begins as seedling	delayed until attainment of full diameter
Leaf survivorship	lower	higher
Ability to grow in shade	higher	lower
Response to large canopy opening	lower	higher
Max. density of reproductive-size individuals in old forest (per ha)	~50	~5
Size of spatial aggregations	small	large

this difference may be related to *Socratea*'s stilt-rooted form in contrast to the more typical palm growth form seen in *Scheelea.*

Demographic analyses suggest that *Socratea* populations may be maintaining themselves under current conditions in the old forest on BCI. However, the extreme dry season of 1983, associated with the El Niño event that began in October 1982, resulted in approximately 12% mortality in the *Socratea* study populations; such levels of mortality are inconsistent with the persistence of *Socratea* populations in this forest. Because the age of the old forest on BCI is probably several times that of the maximum lifespan of an individual *Scheelea,* it appears likely that *Scheelea* is also maintaining itself, but *Scheelea* population dynamics are more difficult to assess due to seed dormancy, slow growth of suppressed individuals, and wide spacing of reproductive adults.

Preliminary analyses of spatial relationships within populations of the two species indicate that *Socratea* shows aggregation at much smaller scales than does *Scheelea.* Information on spatial patterns of the two species are consistent with the interpretation that *Scheelea* requires large gaps in the canopy, while *Socratea* may grow to maturity through closed forest or in small gaps.

This study demonstrates that an understanding of plant growth form contributes to an understanding of the factors that produce population level patterns. An understanding of the ecological significance of plant growth forms is useful in interpreting the possible significance of within- and between-species differences in plant architecture.