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BRIEF COMMUNICATION

GEOGRAPHIC PARTHENOGENESIS IN A TROPICAL FOREST TREE[1]

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As evidenced by embryological studies, certain tropical tree species can reproduce asexually via seed; however, it has generally been assumed that such apomictic reproduction is facultative. Here I report the existence of a population of the lowland Malaysian rain forest tree *Garcinia scortechinii* King that consists entirely of pistillate individuals (40 female trees and no male trees recorded within a 25-ha area). This constitutes the first documented observation of a geographically segregated, obligately asexual population among wild tropical trees. Six additional *Garcinia* species showed a trend toward female bias relative to other dioecious tree species studied, an observation that is consistent with facultative apomixis. The more surprising result for *G. scortechinii* runs counter to the generalization that obligate apomicts occur only in environments in which the absence of competitors might enable persistence of taxa that lack genetic recombination through mixis.

Key words: apomixis; Clusiaceae; *Garcinia*; geographic parthenogenesis; sex ratio; tropical trees.

The ecological importance of biotic interactions in the tropics has generally been thought to predispose tropical trees toward an outcrossed breeding system (Bawa, Perry, and Beach, 1985). For example, while dioecy is relatively infrequent in temperate zone plants, it is quite common among tropical trees (Bawa, 1980), and has been recorded in up to 26−28% of tree species censused in lowland forests of the Sunda Shelf region of Southeast Asia (Ashton, 1969; Thomas and LaFrankie, 1993). The majority of dioecious tropical trees exhibit male-biased secondary sex ratios (Opler and Bawa, 1978; Armstrong and Irvine, 1989; Ackerly, Rankin-de-Merona, and Rodrigues, 1990; Wheelwright and Bruneau, 1992). However, significantly female-biased ratios have also been reported, for example in some neotropical Polygonaceae (Melampy and Howe, 1977; Opler and Bawa, 1978). The overall distribution of reported values spans a remarkably wide range across species, from 1:5 to more than 8:1 (staminate: pistillate) (Thomas and LaFrankie, 1993). Staminate individuals tend to flower at smaller sizes and at more frequent intervals than do pistillate individuals, resulting in male-biased secondary sex ratios (Opler, Frankie, and Baker, 1980; Bullock and Bawa, 1981; Bullock, 1982; Bullock, Beach, and Bawa, 1983; Thomas and LaFrankie, 1993). These observations are consistent with the idea that males have a lower minimal resource cost for successful reproduction (e.g., Thomas, 1996). However, the existence of female-biased sex ratios in certain tropical trees is difficult to reconcile in terms of a reproductive cost argument. One explanation for this pattern is apomixis (Kaur et al., 1978; Kaur et al., 1986; Ha et al., 1988).

The incidence of adventive embyrony in dioecious species in which staminate trees are known to occur has been thought to indicate that apomictic reproduction in tropical trees is facultative (Richards, 1990a). Tests for apomixis based on patterns of allozyme polymorphism also suggest facultative apomixis in certain tropical tree species (Murawski, Dayanandan, and Bawa, 1994; Muraski and Bawa, 1994). However, an alternative possibility is exemplified by North American *Antennaria* (Asteraceae) species. Apomictic populations consisting entirely of pistillate plants are found in some areas, while mixed-sex amphimictic populations predominate elsewhere (Bayer and Stebbins, 1983; Bayer, 1987; Bayer, Ritland, and Purdy, 1990). Among dioecious tropical trees, some of the best embryological evidence for widespread apomixis by means of adventive embryony is in the genus *Garcinia* (Clusiaceae) in Southeast Asia (Treub, 1911; Sprecher, 1919; Horn, 1940; Lim, 1984; Ha, et al., 1988; Richards, 1990a). *Garcinia* is also of interest as a genus in which species are thought to have arisen through formation of allopolyploid hybrids (Richards, 1990b). Although tallies based on herbarium specimens have been made (Richards, 1990a), there is virtually no information on sex ratios in natural *Garcinia* populations. Here I present evidence that *Garcinia* species tend to display sex ratios that are relatively female-biased in comparison with other dioecious rain forest trees, and that at least one *Garcinia* species includes an all-female, apparently obligate asexual population covering a minimum area of ~ 10 km^2.

STUDY SITE AND METHODS

The study takes advantage of a recently established 50-ha forest plot at Pasoh Forest Reserve, Negeri Sembilan, West Malaysia (2°59′N, 102°18′E). This plot repeats the methodology of a similar plot established at Barro Colorado Island in Panama (Hubbell and Foster, 1986b).

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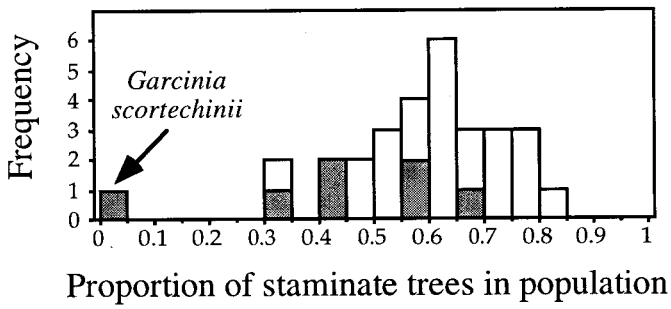

Fig. 1. Frequency distribution of sex ratios in 30 species of primary rain forest trees in a mapped 50-ha forest plot at Pasoh Forest Reserve, West Malaysia. *Garcinia* species, indicated by shaded bars, show an average sex ratio more female-biased than other taxonomic groups surveyed ($P<0.001$: *t* test). Sex ratios are quantified as the proportion of males among all reproducing individuals >1 cm in stem diameter, averaged across reproductive episodes. (The average sample size = 96 reproductive individuals per species per episode.) The other genera include *Aporusa* (Euphorbiaceae), *Baccaurea* (Euphorbiaceae), and *Diospyros* (Ebenaceae). *Garcinia* species examined include *G. bancana* (Miq.) Miq., *G. malaccensis* Hk.f., *G. nervosa* Miq., *G. scortechinii* King, *G. parvifolia* Miq. (common form only: see text), and two undescribed species (*G.* ''dark'' sp. nov. [JVL2781] and *G.* ''small'' sp. nov. [JVL3347]). Information for other taxa, including specimen citations and taxonomic notes, are listed elsewhere (Thomas, 1993; Thomas and Ickes, 1995; Thomas and LaFrankie, 1993).

Every free-standing woody stem >1 cm in diameter was tagged, measured, and identified during the period 1985–1987 (Manokaran et al., 1990). In order to locate flowering populations of selected taxa, monthly phenological observations were made on species in the study genera from January 1990 to May 1993. The all-pistillate population was encountered during the course of a wider survey of sex ratios in dioecious species at the site. A total of 42 censuses were conducted on 30 dioecious species; the total sample size of sexed individuals was 4048. Full details of observations on other species will be presented elsewhere (see also Thomas and LaFrankie, [1993]). Voucher specimens of staminate and pistillate forms for all species are housed at the Forest Research Institute of Malaysia Herbarium (KEP). Populations of flowering trees of a given species were censused throughout subsections (or all) of the 50-ha plot. During censuses, identifications of individual trees were verified, and the presence or absence and gender of floral structures were noted.

RESULTS AND DISCUSSION

Garcinia species tended as a whole toward female bias in comparison with other dioecious trees species studied at Pasoh Forest Reserve (Fig. 1). More remarkably, the population of *Garcinia scortechinii* (King) censused within a 25-ha area consisted entirely of pistillate individuals ($N = 40$: Fig. 2). The odds of such an observation under a null hypothesis of a 1:1 sex ratio are < 1 in 10^{12}. (Correcting for the fact that this observation was made in the course of broader survey [cf., Rice, 1989], the odds are < 1 in 10^{10}.) The majority of flowering *G. scortechinii* individuals also fruited (27 of 40, or 68%). Dissected fruits from these individuals exhibited apparently normal seed development, and seedlings were frequently observed throughout the study plot (Fig. 2; see also Ha, et al., 1988).

A previous survey of herbarium specimens of *Garcinia* in Malaysia recorded no staminate individuals of *G. scortechinii* (Richards, 1990a). I have similarly recorded only

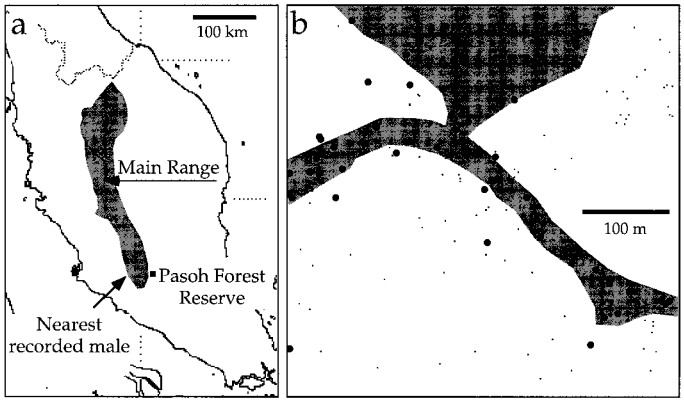

Fig. 2. (a) Location of study site and of the nearest recorded staminate individual of *Garcinia scortechinii*. (b) Spatial distribution of pistillate and nonreproductive individuals of *Garcinia scortechinii* in a 25-ha area at Pasoh Forest Reserve, West Malaysia. Shaded areas in (b) indicate the approximate extent of periodically inundated riparian zones within the plot. Large points indicate pistillate trees; small points indicate nonreproductive juveniles >1 cm stem diameter.

pistillate individuals in and near Pasoh Forest Reserve. However, staminate individuals have previously been described (King, 1890), and several staminate *G. scortechinii* specimens are housed at the Arnold Arboretum herbarium (A). One of these specimens was collected ~50 km from the site of the present study, on the west side of the Main Range in peninsular Malaysia (Gunung Angsi Forest Reserve, Pedas, Negeri Sembilan: FRI 14643; see Fig. 2). In contrast, specimens recorded from the east side of the Main Range were consistently pistillate. These observations indicate at least one purely pistillate population of *G. scortechinii* with a spatial extent of at least 10 km^2, and more probably 10^3-10^5 km^2.

Other *Garcinia* species showing a tendency toward female bias included *G. malaccensis*, *G. nervosa*, and *G.* ''dark'' sp. nov.; however, flowering sex ratios for these taxa were not significantly different from 1:1 (for the May 1990 flowering of *G. malaccensis*, 31 staminate and 48 pistillate trees were recorded: $P=0.055$; *G* test). (Ha et al. [1988] who earlier noted an apparent absence of staminate *G. scortechinii* at Pasoh, also, but erroneously, report an absence of staminate *G. malaccensis*.) The observed tendency toward female bias is consistent with embryological evidence suggesting facultative apomixis in *G. malaccensis* (Richards, 1990a, b). A second possible example of an all-female *Garcinia* population is that of a subset of trees identified as *G. parviflora*. Results of bagging experiments and embryological observations on this taxon (Ha et al., 1988) indicate that the structurally hermaphroditic flowers (i.e., bearing pronounced staminodes) are in fact functionally female and also are capable of producing seed in the absence of pollen. There are, however, at least two distinct forms currently ascribed to *G. parviflora* found at the site: a less-common form studied by Ha et al., in which trees flower almost continuously, producing copious white flowers with reflexed petals, and a more common form flowering at intervals > 1 yr and producing pale yellow flowers with nonreflexed petals. Eight flowering individuals of the first, putatively apomictic, type were located in the pres-

ent study, and all were functionally female; however, both staminate and pistillate individuals of the latter type were found. It is thus likely that *G. parviflora* includes one or more genetically isolated apomictic forms, but further work is needed to confirm this.

The persistence of an obligate apomict in a primary lowland tropical forest is of substantial interest in terms of comparative patterns of parthenogenesis. Previous comparative studies in temperate-zone communities (Bierzychudek, 1985; Asker and Jerling, 1992) have found that apomicts tend to be more common at higher latitudes and higher altitudes, are associated with a history of recent glaciation events, and often have broader geographic ranges than related sexual forms. Temperate-zone research has also suggested that apomicts may generally be more successful as colonists due to the ability to colonize disturbed, marginal habitats from the offspring of a single seed (Stebbins, 1950). The existence of a local geographic parthenogen in tropical lowland rain forest constitutes an obvious and extreme exception to each of these trends. Recent work has also addressed the hypothesis that apomictic plants possess ''general purpose genotypes'' (Lynch, 1984; Bierzychudek, 1989; Michaels and Bazzaz, 1989). However, the distribution of *G. scortechinii* adults shows an association with periodically flooded areas in the 50-ha plot (Fig. 2), suggesting that this apomict is an edaphic specialist.

More speculatively, the existence of a rain forest agamospecies also provides support for a nonequilibrium view of rain forest community structure (Hubbell and Foster, 1986a). If competitive exclusion does not act to eliminate a tree taxon that lacks genetic recombination through mixis, it follows that either: (1) such competitive interactions are very weak, or (2) mixis is not important in maintaining ecological variability that allows for species persistence. This observation also recalls an early speculation by A. Federov (1966) that low population densities of tropical rain forest trees should result in high levels of self-fertilization, resulting in small population sizes and a potential for speciation through genetic drift. Subsequent research has indicated that the majority of rain forest tree species are in fact predominantly outcrossing (Bawa, Perry, and Beach, 1985; Murawski, 1995). However, the present study suggests that Federov's idea may be valid in a somewhat different context: specifically, low population densities of tropical trees may in some cases favor agamospermy as an ''escape from sterility,'' perhaps particularly in taxa that arise as allopolyploid hybrids.

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