

SUMMARY

The reproductive biology of five of the seven species of *Bellucia* (Melastomataceae), a genus of shrubs and small trees, was investigated in Amazonia. Successful fruit-set by *Bellucia* requires floral visitation by bees. The flowers are produced continuously all year, and are visited by a wide variety of female bees, the principal pollinators being *Xylocopa*, *Centris*, *Ptilotopus*, *Epicharis*, *Eulaema*, *Bombus*, and *Oxaea*. The floral attractants are color and the odor produced by the pollen, stamens, and petals; the reward is pollen. Three species of *Bellucia* are self-incompatible. Indiscriminate visitor behavior and lack of phenological, morphological, or genetic barriers lead to hybridization between sympatric species of *Bellucia*, and no more than two species occupy the same habitat at any one locality. *Bellucia* produces berries with numerous small seeds, and is dispersed by birds, bats, monkeys, tapirs, turtles, and ants. Seedling establishment requires full sunlight, and occurs on a variety of soil types. The reproductive strategy is interpreted as that of a pioneer species.

INTRODUCTION

As part of an effort to understand evolutionary relationships in a small group of closely related species, the reproductive biology of *Bellucia* (Melastomataceae) was investigated. This neotropical genus comprises seven species, four of which are medium-sized trees, and the other three shrubs. The species differ from each other in inflorescence position, pubescence, and morphology of the calyx. All but two are common, wide-ranging species. The object of this study was to establish whether these species have diversified in critical aspects of phenology, pollination biology, breeding system, and seed dispersal strategy.

Distribution

The distribution of the seven species is shown in Figure 1. *Bellucia grossularioides*

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occurs from southern Mexico to Bolivia and Mato Grosso, Brazil; *B. pentamera* covers a similar latitudinal span but has a more western distribution and does not reach the Guianas. *Bellucia aequiloba* occurs at the southwestern periphery of the Amazon basin, in Brazil and northern Bolivia; *B. dichotoma* is found in the central and eastern Amazon basin, and one shrub species, *B. acutata*, is confined to the savannas of Brazilian Amazonia, mainly along the Madeira river. A further two shrub species occur in Mato Grosso and adjacent Bolivia, and Terr. Fed. Amazonas in Venezuela, respectively (Renner, in press). *Bellucia* occurs on several islands in the Caribbean where it has been introduced; it has also been introduced in Africa and Asia (Stone, 1972; van Steenis, 1975). Three species occur at elevations from sea-level to between 800 and 1600 meters; the other four are lowland species.

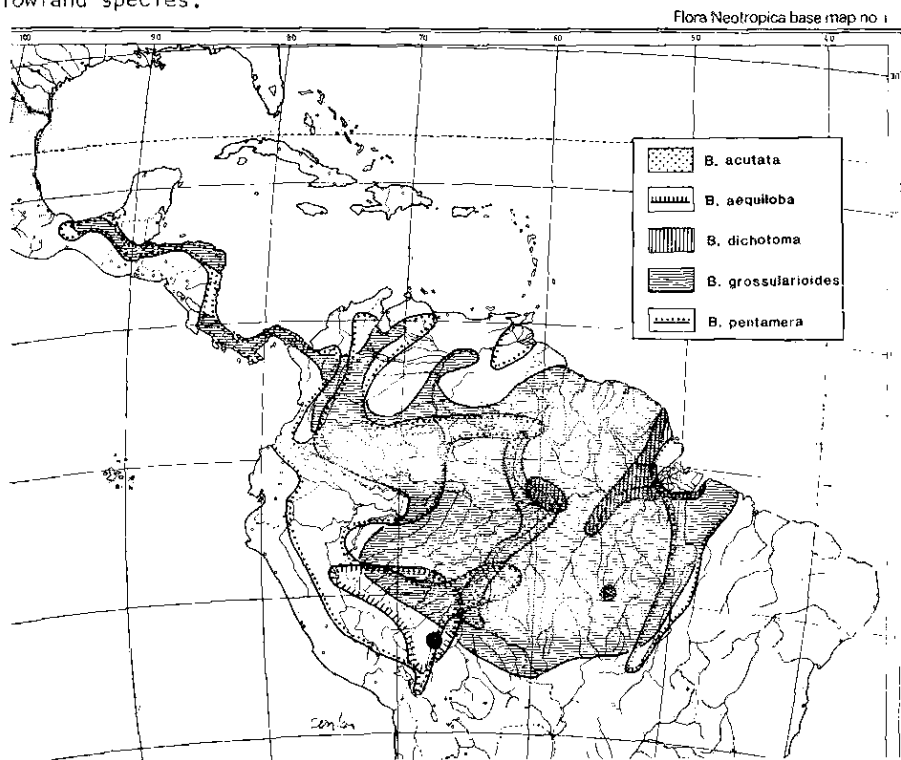


Fig.1. Distribution of *Bellucia*. Two additional species occur in Mato Grosso and adjacent Bolivia and in Terr. Fed. Amazonas in Venezuela, respectively.

The four arborescent species grow in undisturbed and disturbed vegetation, and are tolerant of a range from sandy, well drained to waterlogged (at least for part of the year) soils. The shrubs grow in savannas which are submitted to regular burning and flooding. Logging, road-building, and pasturing have provided excellent habitats for the light-demanding species of *Bellucia*. *B. dichotoma* and *B. grossularioides* are amongst the most important pioneer species in terms of numbers of individuals per area in central Amazonia. In extra Amazonian regions, *B. pentamera* is often found invading newly deforested land.

The species' ranges often overlap but no more than two species occupy the same

habitat at any one locality.

Phenology

The flowering periods of *B. dichotoma*, *B. grossularioides*, and *B. acutata* in the vicinity of Manaus were determined by periodic observations from October 1980 to November 1982 and April 1982 to November 1984. In addition, collaborators of the "Minimal critical size of ecosystems" INPA-WWF project (Lovejoy et al., 1984) collected phenological data for *B. dichotoma* and *B. grossularioides* in the same area from 1981 to 1984.

These three species flowered for lengthy periods or continuously throughout the year. During the beginning of the rainy season from about October to January there was a high abundance of new flower buds but some flowering occurred in all months of the year. Some individual trees of *B. dichotoma* flowered continuously for at least five years; others paused for several months at irregular intervals. Flowering within the species was thus partly asynchronous. In other parts of the range of *B. grossularioides* this species either prefers the rainy season (Croat, 1978; Cavalcante, 1979) or shows no clearcut flowering period (Roosmalen, pers. comm.). According to local residents *B. pentamera*, and *B. aequiloba* flower all year round near Rio Branco and Cruzeiro do Sul (Acre, Brazil). The fruiting phenology is the same as the flowering phenology.

Near Manaus an average tree or shrub of *Bellucia dichotoma*, *B. grossularioides*, or *B. acutata* puts out ten to twenty-five fresh flowers per day.

Floral Morphology and Floral Cycle

All six species have very similar flowers (comp. Fig. 2 A, B). The flowers have five to eight pure white (in *Bellucia dichotoma*) or externally pink-flushed petals which vary slightly in length between the species. The tree species have flowers six to eight centimeters across, while the shrub species' flowers are three to four centimeters in diameter. The buds begin to split open in the evening and by sunrise the petals spread horizontally. Upon opening of the flowers, the ten to sixteen stamens form a compact ring around the style which then bends to the lower (i.e., closest to the ground) side of the flower and comes to lie between two stamens with the stigma protruding from the ring of stamens (Fig. 2 A, B). The stigma is large (about 3-5 mm diam.) and sticky. The stamens are thick and have the anthers turned inward with the two minute apical anther pores pointed slightly inward, too. The stamens are white except for a yellow area externally at the base of the connective. In all species, the petals change color from white to brown on the second day of anthesis. The flowers do not close during the night and the flower parts are shed on the third day.

Fragrance is produced by the petals, the upper part of the filaments, the connective tissue, the upper section of the style, and the stigma (determined by neutral red staining; Vogel, 1963). The pollen has a more or less pale yellow color depending on the species and possesses the same fragrance. The perfume of *Bellucia* has been compared to that of *Convallaria majalis* L. (lily of the valley; Convallariaceae), citronella (*Cymbopogon nardus* (L.) Rendle; Poaceae), or pomarrosa (*Eugenia* sp., Myrtaceae). No odor is perceptible to humans in *Bellucia acutata*, but visitor behavior described below suggests that

some scent is produced by this species also. It is noteworthy that odor intensity is strongest in second day flowers which have changed color from white to brown. No nectar is produced by *Bellucia* flowers.



Fig. 2. A - *Bellucia grossularioides*, petals 22 mm long; B - *Bellucia dichotoma* to the left, petals 20 mm long, held next to a putative hybrid between *B. grossularioides* and *B. dichotoma*.

Breeding Systems

Controlled pollination experiments were carried out with *Bellucia grossularioides*, *B. dichotoma*, and *B. acutata* near Manaus, Brazil. Results are given in Table 1.

Table 1. Results from pollination experiments on *Bellucia* near Manaus (1980-82 and 1984).

<i>Bellucia</i> species	no. of plants	self-pollinated		cross-pollinated		control	
		flowers treated	fruit set	flowers treated	fruit set	flowers treated	fruit set
<i>dichotoma</i>	4	70	00	76	17	80	00
<i>grossularioides</i>	3	12	00	75	5	75	23
<i>acutata</i>	3	19	00	25	12	25	8

The strong self-incompatibility shown agrees with the general finding of Bawa et al. (1985) of self-incompatibility in a majority of the hermaphroditic trees examined in neotropical forests. The tested species were incapable of agamospermy. The wet type of stigmatic surface and the binucleate pollen (Tobe & Raven, 1983) suggest a gametophytic determination of self-incompatibility (Nettancourt, 1977). Artificial pollination between *B. grossularioides* and *B. dichotoma* yielded fruit with few but viable seeds. Putative hybrid trees with intermediate morphological characters were found along roadsides in the vicinity of Manaus. They were vigorous but seemed to have low seed set. Their pollen was viable as judged by a few back-crossing experiments with one parent, which yielded fruits with seeds. Because of the long time period between fertilization, fruit maturity, and seed germination, viability of the seeds was not tested in this last experiment. The hybrids have flowers intermediate between the parents in number of floral parts (Fig. 2 B).

Pollination Mechanism and Pollination

Bellucia grossularioides, *B. dichotoma*, and *B. acutata* were observed for about 80 hours each at different times of the year from October 1980 to November 1982 and from April to November 1984. For *Bellucia acutata* observations were made near Manaus and in the natural savannas at Humaitá (upper Madeira river, Amazonas). *Bellucia grossularioides* was studied near Manaus and in the upper Rio Negro region of Brazil and Venezuela (in March 1985). *Bellucia dichotoma* was observed at Manaus and near Santarém (lower Amazon river, Pará). Limited observations were made on *Bellucia pentamera* near Humaitá and Rio Branco (Acre) and on *Bellucia aequiloba* near Rio Branco.

Bellucia flowers were visited exclusively by female bees which collected pollen as food for their larvae. 27 species belonging to 11 genera were collected from flowers of the five *Bellucia* species (Table 2). Where two *Bellucia* species occurred at the same locality they were visited by the same species of bees.

Nocturnal observations of *Bellucia grossularioides* and *B. dichotoma* showed that wasps (*Apoica pallida*) were the only visitors. They gleaned pollen grains from petals

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Table 2. Bees collected on flowers of *Bellucia acutata*, *B. aequiloba*, *B. dichotoma*, *B. grossularioides*, and *B. pentamera*. For localities see explanation in text.

OXAEIDAE

Oxaea flavescens (Klug)

ANTHOPHORIDAE

Centris lilacina (Cockrell)

Centris sp. nov.

Ptilotopus superbus (Ducke)

Epicharis conica F. Smith

Epicharis rustica (Olivier)

Epicharis affinis F. Smith

Xylocopa frontalis (Olivier)

Xylocopa tegulata Friese

Xylocopa similis F. Smith

HALICTIDAE

Augochloropsis hebescens (F. Smith)

APIDAE

Eulaema cf. *meriana* (Olivier)

Eulaema nigrita Lepeletier

Eulaema mocsaryi (Friese)

Euglossa intersecta Latreille

Euglossa cf. *ignita* Smith

Bombus spp.

Trigona dallatorreana Friese

Trigona recurva F. Smith

Trigona fulviventris fulviventris Guerin-Meneville

Trigona hyalinata branneri Cockerell

Trigona (*Plebeia*) sp.

Melipona fulva Lepeletier

Melipona compressipes

manaensis Schwarz

Melipona rufiventris

Lepeletier

and stamens. Except for bees, no other insects were regular visitors of *Bellucia* flowers.

All bees alighted directly on the stamens and curved their bodies over a few or all of the stamens depending on size. All bees except for those of the genus *Trigona* employed a specific foraging technique to release pollen from the poricidal anthers. They produced vibrations of their thorax with the indirect flight muscles (wings held closed over the back) which were transmitted via the insects' legs onto the anthers and caused a cloud of pollen to shoot out of the anther pores. For this to be effective, a firm grip and close contact between the bee's body and the anthers was essential. Bees used their mandibles, in addition to the legs, to hold onto the external upper part of the stamens, often injuring tissue in the process. Flowers that had been visited repeatedly showed brown necrotic stains on the connectives that would gradually form a ring all around the androecium; these stains are caused by the smaller bees' turning between each buzzing period during a single visit.

Bellucia pollen grains are small (ca 10 μm), smooth, and dry. They adhere to the bees' abdomens and to a minor extent to the rest of their bodies. Thus there is no specificity of pollen placement. Due to their morphology, the bees cannot completely clean themselves, and persistent pollen residues are usually found in a longitudinal line in the center of the abdomen, which is the region where the bee's body, when curved tightly over the androecium, contacts the large, sticky stigmas. At the same time, the stigma is completely covered by the bee's abdomen and thus is protected from the flower's own pollen. Pollen leaves the anthers only when they are vibrated at high frequencies, e.g., 420 Hz, which was the frequency of a tuning fork used to quickly collect large amounts of pollen by simply striking it and holding it to the anthers. Wind does not cause pollen to leave the anthers. Morphological separation of pollen and stigma (herkogamy) completely precludes automatic selfing in *Bellucia* flowers; bee visitations of the flowers are obligatory for fertilization of the ovules.

Both large and small bees vibrated the stamens in the described manner; however, only bees large enough to contact a particular *Bellucia* species' stigma were legitimate pollinators of that species. The very wide range in size of the bees visiting any one *Bellucia* species is illustrated by Figure 3 A.

Trapping behavior was exhibited by *Xylocopa*, *Centris*, *Ptilotopus*, *Epicharis*, and *Eulaema* bees. An easily spotted large (3 cm long) individual with a bright red thorax (*Centris* sp. nov., the third bee from the left in the topmost row in Fig. 3A) arrived at the tree under observation at 8:25, 8:30, 8:32, and 8:37 A.M. on consecutive days.

Analyses of the proportional composition of pollen loads of 13 bees of the five trapping genera mentioned above indicated high fidelity to *Bellucia* on individual foraging flights. These visitors carried almost pure loads of *Bellucia* pollen with a few grains of Myrtaceae, Apocynaceae, Loranthaceae, and Verbenaceae which were probably visited for nectar. Additionally, *Cassia* (Fabaceae) pollen, for which the bees forage in the same manner as for *Bellucia* pollen, i.e., vibrating the poricidal anthers, was present in two cases.



Fig. 3. A - Bees captured on *Bellucia grossularioides* near Manaus (Brazil); B-*Bellucia grossularioides* fruits placed on a leaf; average fruit is 2.5 cm long.

On the average, a *Bellucia dichotoma* tree with seventy to twenty-three open flowers was visited by eight legitimate pollinators per hour during the period (8-10 A.M.) of most intensive bee activity ($n = 8$ hrs on four consecutive days in December 1980). These pollinators normally visited all fresh flowers on a tree before flying on, often to another

individual of *Bellucia* (as indicated by the pollen load composition). Along roadsides and in savannas, individual large bees could be followed with binoculars. Visits to two co-occurring species on the same foraging trip were observed for the pairs *Bellucia grossularioides* - *B. dichotoma* and *B. pentamera* - *B. grossularioides* near Manaus and near Humaitá respectively.

Trigona bees were frequently encountered on *Bellucia* flowers at all localities, but did not vibrate the stamens in order to obtain the pollen. Instead, they were pollen scavengers and robbers (depending on the species), showing a complex behavior described in detail previously (Renner, 1983). *Trigona* bees were sometimes present in great numbers, working on a single flower for several minutes. The large bees did not alight on flowers that had individuals of *Trigona* on them, and thus these pollen scavengers may enhance inter-plant movements of legitimate pollinators.

Flowers of the previous day, distinguishable by their brown color, were not visited except by an occasional *Melipona* or *Trigona* bee. It is interesting to recall that second day flowers had a stronger scent than fresh flowers. Bees probably used scent in addition to visual clues to find the flowers. This became obvious when flowers of *Bellucia acutata*, that had been bagged in the bud stage with insect-proof white gauze the evening before anthesis, were approached by bees during the morning they opened even though the flowers were not visible.

Fruit Dispersal

Bellucia fruits are pale green to yellow semi-globose berries about 2-3 x 2.5-3.5 cm in size (Fig. 3 B). Their slightly mucilaginous pulp contains about 3000 small (0.5-1 mm long) brown seeds. Hypanthia of fertilized and unfertilized flowers persist unchanged for eight to 25 days before development or abscission occurs. Fruit ripening is completed in about eight weeks and the seeds take five to twenty-five weeks to germinate. Because of the almost continuous flowering of *Bellucia* plants fruits are available over most or all of the year in any particular area of the genus' range.

The berries have a faint, fruity odor and sweet, slightly astringent taste. They are taken by a wide range of animals: monkeys (M. Roosmalen, pers. comm.), birds (pers. obs.), and bats (S. Marquez, pers. comm.), and — once they have fallen to the ground — by tapirs (label data), turtles (M. Roosmalen, D. Moskowitz, pers. comm.) and ants (pers. obs.). The fruits have been fed to monkeys and hogs and are sometimes eaten by humans.

Birds are not the principal consumers and seed dispersers of *Bellucia*; the fruits' position, size, color, scent, and taste indicate that they are most effective at attracting mammals. The relative importance of the different disperser classes will be an object of future studies.

In repeated experiments germination rates of the seeds were low (ca. 1%). *Bellucia* saplings are light-demanding and attain reproductive maturity in four years.

DISCUSSION

Although extended flowering is not uncommon among tropical plants, continuous flowering, such as here documented for *B. dichotoma*, is rare (Janzen, 1967; Hallé et al., 1978). Other species of *Bellucia* also flower for extended periods, and clear-cut flowering periods are absent in all of them. *Bellucia* individuals, having reached the reproductive stage, invest a large part of their energy into almost continuous production of flowers and fruits. Self-incompatibility, shown for the three species whose breeding system was tested, is generally regarded as disadvantageous for colonizing species such as the members of *Bellucia*; this may be balanced by the very high number of seeds per fruit, which makes simultaneous germination of several seedlings at a new site likely. Provided flowers are visited repeatedly, the sticky, large stigmatic surface may enhance reception of the amount of pollen needed to fertilize the numerous ovules and increase chances for pollen from different parents to be received. Obligate outcrossing in self-incompatible tropical tree species often is correlated with a high proportion of big, traplining bees among their flower visitors (Frankie et al., 1983).

The pollination syndrome found in *Bellucia* and all lowland melastomes observed so far (Renner, 1984 a, b) has been described in recent years from a number of other plant species with poricidal anthers (see Bruchmann, 1983, for a review). The majority of these plants have stamens which release pollen only when vibrated by bees. Applied to *Bellucia* flowers, vibrating stamens is an efficient method for the bees to quickly gather large amounts of pollen, particularly because bees are able to start pollen harvesting immediately upon landing. *Bellucia* is different from many bee-pollinated flowers of other plant families, in that the stamens not only provide visual and olfactory clues but at the same time a landing platform; thus no orientation or further walking are necessary once the bee has landed. Pollen release and stigma receptivity are simultaneous in these flowers.

There is no indication of partitioning of pollinator resources by the sympatric *Bellucia* species. One may speculate that the conservatism in floral morphology in *Bellucia* is the result of stabilizing selection, with their shared pollinators being the selective agent. The lack of divergence in floral morphology and the lack of temporal separation of the sympatric species' flowering periods, together with the observed indiscriminate visitor behavior and lack of genetic interspecific barriers (at least in some sympatric species), result in constant hybridization. However, as noted again recently (Carson, 1985), the genetic coherence of a (plant) species' gene pool will not be seriously threatened by interspecific hybridization.

Species of *Bellucia* are characterized by superior reproductive ability and means of dispersal. They are specialized for occupation of transient habitats in physiological features such as their seedling's light requirements and ability to establish on a variety of soil types, and in vegetative traits such as the fast growth of the light wood. It appears that species occupying early phases in succession have a high reproductive effort, in this case in the form of a very large number of seeds, and a correspondingly high intrinsic rate of natural increase: *r*-selected species in the sense of MacArthur and

Wilson (1967). Most species of *Bellucia* can be regarded as tropical weeds; their populations grow predominantly in situations disturbed by man and with man's help *Bellucia* has spread to the Caribbean and the Old World tropics.

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RESUMO

Foram investigadas, quanto à biologia reprodutiva, cinco das sete espécies de *Bellucia* (*Melastomataceae*), um gênero de arbustos e árvores de pequeno porte na Amazônia. Para as plantas de *Bellucia* produzirem frutos, é necessário haver a visita de abelhas às flores. As flores são produzidas o ano todo e são visitadas por uma variedade de abelhas femininas, sendo os principais polinizadores as abelhas dos gêneros *Xylocopa*, *Centris*, *Ptilotopus*, *Epicharis*, *Eulaema* e *Oxaea*. As flores atraem pela cor e pelo odor produzido pelo pólen, pelos estames e pelas pétalas. As abelhas são recompensadas com pólen. Três espécies de *Bellucia* são auto-incompatíveis. Devido às visitas indiscriminadas pelos visitantes, e à falta de barreiras fenológicas, morfológicas ou genéticas, ocorre com frequência a hibridação entre espécies simpátricas. Nunca foram encontradas mais de duas espécies no mesmo habitat em cada uma localidade. O fruto de *Bellucia* é uma baga com pequenas e numerosas sementes dispersadas por passáros, morcegos, macacos, antas, jabotis e formigas. As plântulas requerem sol pleno para se estabelecerem e crescerem sobre vários tipos de solo. Consideramos a estratégia reprodutiva como sendo a de uma planta pioneira.

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