REPRODUCTIVE BIOLOGY OF BROMELIACEAE IN THE ATLANTIC RAINFOREST OF SOUTHEASTERN BRAZIL

Gustavo Martinelli

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A thesis submitted to the
University of St. Andrews for
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School of Biological and Medical Sciences
University of St. Andrews
October 1994

To Cecilia, Gabriel, Tomaz and Olivia and in the memory
of Joao Eulálio Cesario Alvim who died when visiting us.

DECLARATION

I, Gustavo Martinelli, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment or any other degree or professional qualification.

[redacted]

Gustavo Martinelli

October 1994

STATEMENT

I was admitted to the Faculty of Science of the University of St. Andrews under the Ordinance General No. 12 on October 1991 and as a full-time candidate for the degree of Ph.D. on October 1992.

[redacted]

Gustavo Martinelli

October 1994

CERTIFICATE

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the Ph.D.

Signature of Supervisor

[redacted]

P.E.Gibbs
October, 1994

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Gustavo Martinelli

October 1994

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ABSTRACT

A study was made of the reproductive biology of 35 species of Bromeliaceae in the Atlantic Rainforest province of southeastern Brazil. Three study sites were established, at different altitudinal levels ranging from the sea coast to 1800m, and including a range of forest types and high montane grassland.

The studied taxa included 18 species of Vriesea, five of Quesnelia, two of Pitcairnia, two of Nidularium, two of Neoregelia, two of Billbergia, two of Aechmea, one of Dyckia and one of Tillandsia.

Aspects of flowering phenology, pollination biology, breeding system and fruit-set success were studied for 14 species, whilst less complete data, usually limited for breeding system and fruit-set, was obtained for further 21 species.

The flowering phenology of the bromeliad species showed a displacement towards the wet, summer period between November-February, with many species showing overlapping flowering at this time, and thus with little evidence of adaptative phenological displacement.

The species could be grouped into two pollination guilds, hummingbirds and bats, with the former predominanting, such that 26 of the 35 species had this vector, whilst seven species, with nocturnal anthesis and scented flowers, were visited by bats. For both kinds of vectors, the flowering strategy known as 'steady state', in which few flowers are opened per day/night over a long period, was the commonest situation encounted, since 'steady state' flowering has been associated with so-called 'traplining' pollinator, in which the vector regularly forages along a sequence of plants.

Hand-pollination experiments showed that the majority of species were self-compatible, with fluorescence microscopy studies evincing massive self-pollen germination on the stigma, with growth of pollen tubes to the ovary

and high levels of ovule penetration. However, six species were considered to be self-incompatible, and it is of interest that all of these taxa are member of the subfamily Bromelioideae.

Despite the prevalence of self-compatibility, it is likely that a 'mixed-mating' system, with some outcrossing occurs in many species because of the 'steady state' type of flowering, and also the marked protandry of the flowers at anthesis.

CHAPTER 1. INTRODUCTION

1.1. BROMELIACEAE

The Bromeliaceae is a large and predominantly neotropical family with some of 54 genera and over 3000 species, all restricted to the New World except for one species, Pitcairnia feliciana, which occurs in West Africa (Smith & Downs, 1974, 1977, 1979; Luther & Sieef, 1992).

Species of the Bromeliaceae first became horticulturally important during the nineteenth century, but their introduction to the western world started with specimens of "pineapple" over three hundred years earlier, with Christopher Columbus' second voyage to the New World in 1493 (Hayward, 1956; Collins, 1960; Benzing, 1980). In 1535, Oviedo produced the first illustration of a fruiting species of Ananas. A more detailed description of "pineapple" was produced by Rumphius in 1590, both redrawn by Benzing (1980) and Gortan (1991).

Linnaeus (1753) recognized the genera Bromelia and Tillandsia and listed fourteen species under these genera, whilst Jussieu (1789) elevated the genus Bromelia to family level as "Bromeliae". By the 19th century, many species began to arrive in England, Germany, Belgium, France and others countries of Europe, and many such introductions were first described, especially in Belgian and English publications such as *La Belgique Horticole, Revue Horticole* and *L'Illustration Horticole,* or were illustrated and described in Curtis' *Botanical Magazine, The Botanical Register, The Botanical Cabinet*, and other journals.

Among the collectors of this period were Linden, Wallis, Griesbrecht, and the largest collections at this time were in Belgium such as that of Makoy in

Liege. The authority on the family was also Belgian: Charles Morren. Two of Morren's students were Andre and Mez, both of whom became authorities on the family following Morren's death.

Andre made a major collecting expedition to Colombia and Ecuador during the period of 1875-77 and on his return published a monograph *Bromeliaceae Andreanae* in which he described and illustrated 122 species and 14 varieties of which 91 were new. The other student of Morren's, Carl Mez, monographed the Brazilian species in Martius's *Flora Brasiliensis* (1891-94) and subsequently the whole family in De Candolle's *Monographiae Phanerogamarum* (1896) and in Engler's *Das Pflanzeinreich* (1935). The latter was the most complete monograph on the family up that time, remaining the most authoritative work on Bromeliaceae for the next forty years. Another major contribution was the monograph made by Harms (1930) to the series of Engler & Prantl's *Die Naturlichen Pflanzenfamilien*.

By 1935, Mulford B. Foster, had made a number of expeditions to South America, and was responsible for collecting and introducing a great number of species of Bromeliaceae to the United State of America. Based on the Foster's collections and more recent material, Smith (1955) published a monograph of the Bromeliaceae of Brazil, and subsequently, Smith & Downs (1974, 1977, 1979) published the most complete systematic treatment of the family, issued in three volumes of the *Flora Neotropica* series.

As pointed out by Smith (1974), the taxonomy of Bromeliaceae has been largely morpho-geographical, and the family is divided in three subfamilies based mainly on seed characteristics: in the subfamily Pitcairnioideae, the seed has an appendage which is entire or slightly divided or the appendage is lacking; in this group the fruits are usually dehiscent, the leaves mostly spinose-serrate, and the plants are usually terrestrial. The subfamily Tillandsioideae has a seed-appendage which is finely divided and forming a coma; the fruit is dehiscent, leaves always entire, and the plants mostly epiphytic. In the subfamily Bromelioideae the seeds lack an appendage, the fruit is baccate with ovary inferior or nearly so, leaves mostly spinose-serrate, and the plants are terrestrial or epiphytic.

The family Bromeliaceae is morphologically and anatomically distinct and is placed in the monocotyledoneous Order Bromeliales, in which it is the only family. The affinities of Bromeliaceae are uncertain. Some authors agree that Velloziaceae is probably the sister taxon to the Bromeliaceae (Huber, 1977; Dahlgreen & Clifford, 1982; Thorne, 1983; Gilmartin & Brown, 1987; Beaman, 1989). Hutchinson (1934) proposed that the Bromeliaceae has affinities with Amaryllidaceae, Cronquist (1968) with the Commelinaceae and Zingiberaceae, and Smith (1934, 1974) suggested a relationship with the Rapateaceae.

1.2. MORPHOLOGY AND ANATOMY

Roots are usually present and always adventitious, but frequently serving merely as holdfast in the epiphytic and saxicolous species, with little or no role in the absortion of water and nutrients. Terrestrial species take up water and nutrients from the soil via the root system in all stages of development. (Downs, 1974).

The stem of Bromeliaceae species is often short and compact, although the diameter of the vegetative leafy-stem ranges from one mm in Tillandsia usneoides to stout, erect and rather woody stem, around 1 m or more in Puya raimondii. In some taxa specialized stoloniferous stems are present which arise from older leaf axils, with a new rosette initiated at the tip of the stolon. (Benzing, 1980).

The leaves are usually in a dense cluster, long and parallel-veined, rigid and spinulose-toothed or flaccid and without spines, spirally arranged, most commonly rosulate on the short or elongated stem, with tight, imbricate and broad sheaths which form a cup or a vase within which rainwater accumulates. Typically, the leaves of species of Bromeliaceae present small-lumened epidermal cells which have a very thick cuticle and thickened inner walls. (Downs, 1974).

The colour of the leaves may be green, grey-green to reddish or reddish-brown, and frequently purple on the underside or cross-banded, spotted with silver, black, red or maroon. The red to purple coloration is due to anthocyanins in the hypodermis and sub-epidermal water storage cells (Downs, 1974). The rather unique flavonoid composition of the leaf tends to confirm the isolated position occupied by Bromeliaceae in the Monocotyledons. (Williams & Harborne, 1988).

The presence of trichomes or scales on many leaf surfaces is one of the most interesting aspects of the Bromeliaceae, since these features are significant in the water economy of many species and more attention has been given to the squamiform scale than to any other structure of the family (Downs, 1974). The water-absorbing scales or trichomes have a central disc of cells with thick upper-walls, while the scale wings function as capillary structures to bring moisture to the disc cells by capillary action between the scales and epidermis (Mez, 1904; Downs, 1974). The leaf scales in the Bromeliaceae have been studied by Mez (1904), Billings (1904), Keiline (1915), and more recently by Tomlinson (1969), Downs (1974) and Benzing (1976, 1980).

The basal rosette of leaves is the most characteristic vegetative feature of Bromeliaceae, since it forms a series of "water-tanks". The tanks of many Bromeliaceae species are capable of holding considerable quantities of water and litter (McWilliams, 1974; Benzing, 1980). The tanks vary in shape and proportions, according to the size, form, and position of the spreading leaves. Tanks can be divided in two basic types: funnelform, in which the largest leaves are positioned spirally or in two upright ranks which form a single chamber in the centre of the rosette, as in species of the genera Billbergia, Quesnelia, and Aechmea. A second type of rosette is tubular with long tanks that hold water and McWilliams (1974) has suggested that such tanks are more effective against the evaporation. Benzing

(1980), however, has indicated that the adaptative advantages of each type are unclear.

The inflorescence is usually terminal from the main axis and comprises a raceme or spike. True terminal flowers do not occur, although certain species (e.g. Tillandsia usneoides) produce a single pseudo-terminal flower. The great ornamental and horticultural value of many Bromeliaceae is due to the beautifully coloured scapes and bracts of the inflorescence (McWilliams, 1974; Benzing, 1980).

The flowers are usually hermaphroditic but occasionally unisexual (Cryptanthus), regular or slightly irregular, and almost always trimerous. Exceptions are Guzmania fuerstembergiana and Dyckia odorata which have dimerous flowers, and Billbergia nutans which sometimes presents a few tetramerous flowers (Smith, 1974; Downs, 1974).

The perianth is differentiated into three-sepals and three-petals, with the calyx is frequently twisted to the left so that the sepals have the right margins covered. The corolla is usually twisted to the right. The petals are free or connate, linear to ovate, entire or finely crenate to denticulate, with the apex rounded, retuse, apiculate or mucronate. The colour may be white, red, purple, blue, yellow, orange and brownish (Downs, 1974).

A very characteristic feature of the petals is a ligular scale-like appendage at the base. This structure is used as a character to distinguish some species in Pitcairnia, and to distinguish between the genera Vriesea, which has such appendages, from Tillandsia, which does not. The structure may be a simple membranaceous scale, or may be formed of two separate scales, and is usually serrate or lacinate (Downs, 1974).

Brown & Terry (1992) studied the morphology of the petal appendage using light and scanning electron microscopy, and stated that the morphological variability in this appendage may be useful, together with other characters, to delineate species or species alliances. These authors considered that the morphological variability of the petal appendages had been under-utilized as a taxonomic character. They pointed out, however, that it is difficult to use this character in most herbarium specimens because the appendages are poorly preserved, and that fresh or liquid-preserved flowers are needed.

Studies on floral development of bromeliad species has shown that the petal appendage is the last external, multicellular structure to be formed in the flower. Their development coincides with the final maturation and enlargement phase of the flower, as pointed out by Brown & Terry (1992). These authors, explained that "in virtue of their terminal ontogenic nature, the scale would be predicted to have greatest taxonomic utility at the specific or subspecific level".

Harms (1930) proposed that the function of the petal appendages is to help the prevention of nectar loss and suggested that the evolution of two more or less separate petal appendages can be explained by the pressure of filaments on a single ligular primordium. McWilliams (1974) agreed with the function proposed by Harms (1930) and suggested that these structures determine the height at which the nectar is contained into the flowers. Varadarajan & Brown (1988) concluded that in some taxa of the subfamily Pitcairnioideae the petal appendages are vestigial and non-functional, despite the fact that in some taxa of Pitcairnia they are functionally presents as "nectariferous scale" and help in nectar retention.

Stamens are in two whorls of three. In corollas with connate petals, the filaments are more or less adnate with the petals. The filaments are frequently narrowly ribbon-shaped and the epipetalous filaments generally lie between the scales or longitudinal folds when petal appendages are present. In Dyckia and Bromelia they may be undulate-folded as in many species of Tillandsia (Downs, 1974). Evans & Brown (1989) observed that the plicate staminal filaments of some Tillandsia species may form a barrier similar to the petal appendages within the floral tube, and so perhaps retard nectar evaporation.

The stigma in Bromeliaceae has only recently been considered to be of significant taxonomic importance by Utley (1983), Brown & Gilmartin (1984, 1988,

1989) Varadarajan & Brown (1988) and Gortan (1991). Brown & Gilmartin (1989) used scanning electron microscopy to observe stigmas and classified stigma morphology in five categories: (a) conduplicate-spiral, (b) simple-erect, (c) cupulate, (d) convolute-blade, and (e) coralliform. These authors observed that in the subfamily Bromelioideae, the stigma is nearly always of the conduplicate-spiral form, with exception of the genera Cryptanthus and Orthophytum. In the subfamily Pitcairnioideae, of 71 taxa studied by these authors, 64 had the conduplicate-spiral stigma, with exceptions occurring in Brewcaria, Brocchinia (partially), Cottendorfia and Fosterella. In the subfamily Tillandsioideae, all five stigma types are encountered but 116 of the 224 species examined also showed the conduplicate-spiral stigma morphology. These authors suggested that within this latter subfamily stigma variability appears to be a most useful taxonomic character.

The ovary is superior to half-inferior in the subfamily Pitcairnioideae, superior in Tillandsioideae (except Glomeropitcairnia), and inferior in Bromelioideae. The ovary consists of three carpels which are more or less fused at the margins (Downs, 1974).

The nectaries in the Bromeliaceae are rather curious and occur on the septa dividing the ovary locules. In a study of morphological variation of floral features of the subfamily Pitcairnioideae, Varadarajan & Brown (1988) examined the septal nectaries in a range of species which presented superior ovary to inferior ovary conditions, and they found that the septal nectaries usually consist of three longitudinal systems of the channels in the septa that are connected with the axis by a median component and that the channels originate at the ovary base and open where the nectar collects through small slits or rounded pores in the ovary wall as observed earlier by Budnowski (1922), Daumann (1970), Böhme (1988) and Bernardello et al. (1991).

The placentae are usually axillary, extending to the length of the locule. The ovules of Bromeliaceae are frequently anatropous with two very similar integuments, each of which consists of two layers of cells. However, many taxa lack this feature. The characteristic of the seed appendages are considered as a generic and subfamilial character. The embryo is small, and located at the base of the copious, mealy endosperm. (Downs, 1974).

The fruit and seeds of bromeliads provide significant characters which separate the three subfamilies: the Pitcairnioideae, with the fruit generally capsular, usually septicidal, and with seeds of many species with entire appendage, that are dispersed by wind. The genus Navia is an exception, with no appendage; the Tillandsioideae with capsular fruit and plumose seeds dispersed by wind , and the Bromelioideae in which the ovary is inferior, the fruits baccate and with naked seeds, despite the fact that the ovules present various type of appendage. Downs (1974) observed that the outer integument is absent in mature seeds and "has probably transformed into the sticky and gelatinous mass found inside the fruits".

1.3. DISPERSAL

Although Harms (1930), Smith (1934), McWilliams (1974) and others have commented on the involvement of birds in the evolution of dispersal mechanisms in Bromeliaceae, the literature on the bird species and mechanisms is scarce. Abendroth (1965) observed that the baccate fruit of Bromelioideae is important item to the diet of the tanager Tachyphomus coronatus, and McWilliams (1974) suggested that there is a high probability of coevolution between some Bromeliaceae and the animals involved in seed dispersal, and that many taxa of the subfamily Bromelioideae present a wide range of variations in colour, size, shape and sugar content in their baccate fruits that are the major factor involved in animal dispersal.

Harms (1930), indicated that the bat Glossophaga soricina disperses seed of several Billbergia species, including Billbergia zebrina whose fruits and seeds have a very strong odor that attracts bats. This agrees with McWilliams' (1974) observations that Billbergia zebrina was largely limited in its distribution to knot holes left in trees by the fallen limbs, and that the bromeliad's growth in this striking habitat, at an angle of 45° from the tree, was due to seeds transported by bats to such knot holes.

The anatomical nature of the appendage or false pappus found in the subfamily Tillandsioideae has been investigated by McWilliams (1974), who compared the effectiveness of dispersal mechanisms of selected Compositae and Bromeliaceae, and concluded that the seeds of Tillandsia fasciculata and Guzmania monostachia were more efficient at remaining airborne than those of Taraxacum officinale and Eupatorium species. This author also noted that the Tillandsioideae has the greatest geographical range compared with the subfamilies Bromelioideae and Pitcairnioideae, noting that all of the bromeliads species native to Florida (USA) belong to this subfamily.

McWilliams (1974) listed the seed weight and estimated total seed production per plant for several self-pollinated bromeliads cultivated in a glasshouse, and found differences in weight of the seeds between species of Bromelioideae that are dispersed by birds, and Tillandsioideae that are wind dispersed.

Salisbury (1942) also noted differences between species that grew in the shade, and sun species, the former having larger seeds, and attributed this difference to the higher level of stored food in large seeds which are utilized in growth and respiration during the dispersal and establishment under low light intensities. Veloso (1952), observed that species of Bromelioideae usually tend to grow under lower light conditions and higher humidity conditions than those of Tillandsioideae.

Grubb et al. (1963) noted that 70-80% of the Bromeliaceae in montane habitats in Ecuador were small and immature, whereas a much lower percentage of such species appeared to be immature in the lowland rainforest, indicating a periodicity in seedling establishment in the former community. The observations of Grubb et al. (1963), and those made by McWilliams (1968,1974), indicate a very definite pattern of cyclical establishment due to the narrow range of tolerance of the seedlings of such saxicolous species, so that the chemical and physical characteristics of the rock substrate appear to be critical for species establishment. Bromeliads do not appear on recently exposed granite until the rock has weathered for a long period. (McWilliams, 1968).

For the majority of Bromeliaceae, the seeds lose their viability relatively quickly, but seed of some xerophytic bromeliads have remained viable for over a year when maintained in laboratory conditions.

1.4. FLOWERING DEVELOPMENT AND PHENOLOGY

The time necessary for the development of the inflorescence following its initiation varies greatly without apparent correlation with genera or subfamily (Downs, 1974). The period required for all flowers of the inflorescence to open may vary between one day (Tillandsia usneoides), 2-3 days in species such as Billbergia pyramidallis (Downs, 1974), or 71 days in Vriesea imperialis (personal observation).

For the inflorescence to extend completely from the tank formed by the leaf sheaths is slow, and Downs (1974) observed that Billbergia elegans required 29 days to get above the water-tank, requiring then only four additional days to begin the anthesis of the first flower, with an average of 10 cm per day. This author did not indicate whether these measurements are made under natural conditions, or with plants under cutivation in a glasshouse. Vriesea imperialis, require c. 84 days from the beginning of development of the inflorescence to the anthesis of the first flowers in natural conditions (personal observation).

Generally, the flowering sequence is from below to upwards with the lowest flower opening first and from outside to inside in case of head or complanate type inflorescences. The exceptions are the genus Canistrum where the middle region flowers first, and in Aechmea calyculata and Vriesea gigantea, in which anthesis occurs first in the center and proceeds upwards and downwards (Downs, 1974).

Details of floral events at anthesis are poorly known for most Bromeliaceae. Recently, Utley (1983) provided excellent descriptions of some species of Vriesea (Tecophylloid group) with regard to their phenology and flower development. Gardner (1986) described anthesis of some species of Tillandsia, and Sazima et al. (1989) provided information for the anthesis of Encholirium glaziovii. Araujo et al. (unpublished data) described the anthesis of Vriesea ensiformis, Vriesea carinata and Vriesea incurvata in a study of pollination biology of these species. Generally, the Bromeliaceae include examples of the three of five flowering phenological types ("steady state", "cornucopia" and "big bang") described by Gentry (1974) for neotropical Bignoniaceae.

1.5. POLLEN

A comprehensive and simplified description of the pollen grains of the Bromeliaceae was produced by Erdtman & Praglowski (1974), based on an investigation of about 125 species of 40 genera. They subdivided the family in two groups, according to the pollen morphology: a) with 1-colpate pollen grains and b) with porate grains, with more than one aperture, and stated that in general terms, the pollen grains are single, or rarely, united in tetrads (in Androlepis).

1.6. CHROMOSOME NUMBER

Chromosome counts have been reported in the literature for only a small proportion of the family. Bromeliads presents several problems for the cytologist, because the chromosomes are very small, stain poorly, and in Tillandsioideae there are chromosome size differences which give two size classes within the complement. The Bromelioideae also show this bimodal complement to some extent, but in Pitcairnioideae, the chromosomes are uniform and very small (McWilliams, 1974).

Lindschau (1933) pioneered the investigation of Bromeliaceae chromosomes, reporting 47 counts and attempting to relate the work with the evolution of the subfamilies. This author indicated that subfamily Bromelioideae has many species with 2n=54, and she stated that the base number of the family was x=9. Gauthe (1965) and Weiss (1965), using sectioned root-tip material, confirmed a number of Lindschau's counts and added many new ones, reporting three series of chromosomes numbers with base number of x=8, 9 and 25. Marchant (1967), worked with meiotic chromosomes, agreed with the earlier authors and published excellent photographs.

McWilliams (1974) reported five new chromosome counts and proposed that the Bromeliaceae had an ancestor with the base number of x=8, with the hypothesis that the Pitcairnioideae is the most primitive subfamily. This author noted that polyploidy is present in the family in the genera Dyckia, Ananas, Bromelia and Tillandsia, mentioning that the only triploid taxa observed have been cultivars of Ananas comosus.

More recent studies on chromosomes of Bromeliaceae have been made by Brown & Gilmartin (1983, 1986, 1989) and Till (1984). These authors revised the work or early authors, showing the great variability in mitotic chromosomes reported, and the lack of concordance between mitotic and meiotic numbers for some taxa within the family, and they pointed out that the variability in mitotic number is reflected in the variable interpretation of chromosome base number for the family.

Brown & Gilmartin (1986) summarized the previous controversy over the base number determination for Bromeliaceae, and discussed the current level of knowledge concerning polyploidy, chromosome size bimodality, and the correlation of non-concordance in meiotic and mitotic chromosome number with taxa with the epiphytic mode of growth. Brown & Gilmartin (1989) presented a model for chromosome base number evolution for Bromeliaceae. They outlined a hypothesis in which the evolutionary model is disbasic and involves hybridization and polyploidy of palaeoploid base number $x=8$ and 9 to yield a palaeotetraploid $(n=17)$.

1.7. EPIPHYTISM AND EVOLUTION

More than half of bromeliad species are epiphytes, often growing in very xeric environments, and such taxa attracted considerable attention in the earlier researches on the biology of epiphytism. The earliest author was Schimper (1885), who noted three basic types of Bromeliaceae: terrestrial plants, epiphytes which hold water in their leaf rosette, and extreme epiphytes which absorb atmospheric moisture and dew from their leaves. After observing the functional morphology of roots and scales of the leaves, he concluded that the evolution of epiphytic habit had occurred within the rainforest itself. Schimper visualized the origin of epiphytism in Bromeliaceae as proceeding by a series of steps from the forest floor to the lower tree limbs, and subsequently into the relatively dry, upper canopy of the forest, as certain species became progressively more independent of roots through increasing specialization of the absorbing trichomes or scales.

Pittendrigh (1948), studied the ecology and distribution of Bromeliads in Trinidad, and agreed with Schimper with regard to the origin of epiphytism in the subfamily Bromelioideae, with both terrestrial taxa such Ananas, Bromelia, Cryptanthus, Orthophytum and Greigia, and facultative epiphytes which are frequently found on rocks or trees, which include species of Aechmea, Billbergia, Canistrum, Neoregelia and others. Pittendrigh concluded that species of Tillandsioideae had entered the rainforest as light-demanding xerophytes in the uppermost levels of the canopy, and then subsequently invaded the lower levels where light intensity is lower. Pittendrigh supported this argument by a consideration of floral morphology, which was regarded as being most primitive in

Tillandsia. This evolutionary interpretation by Pittendrigh was in conflict with the anatomical evidence of Tomlinson (1969) who pointed out that on the basis of scale morphology, the genus Tillandsia is clearly the most specialized genus in the Tillandsioideae.

Smith (1934) hypothesised that the genus Pitcairnia represents a "evolved peak" in the subfamily Pitcairnioideae due to the series of derived characters in this group, such as semi-inferior ovary and seeds with a caudate appendage, well adapted to wind dispersal. Smith proposed that Pitcairnia had evolved recently within their subfamily, since the distributional area of this genus is twice that of any other genera of Pitcairnioideae, presumably due its ability to grow in the rainforest.

1.8. GEOGRAPHIC DISTRIBUTION

The Bromeliaceae ranges from Virginia in the USA to Patagonia, in the south of Argentina, and from Juan Fernandez Island in the Pacific to eastern Brazil. Only a single species of Pitcairnia is found in West Africa. Species of Bromeliaceae are found in a variety of habitats over this vast geographic range Hutchinson (1959) and Smith (1974), observed that this very unequal, disjunct range, is rather closely paralleled by the supposedly related Rapateaceae.

Smith (1974), however, pointed out that although their African extension has been doubted or ignored, the Cactaceae are a much closer parallel to the Bromeliaceae than are the Rapateaceae. The range of Cactaceae in the Americas is even larger than that of the Bromeliaceae, and they have also developed forms adapted to the extreme aridity and extreme humidity, although this latter aspect is frequently overlooked. Like the Bromeliaceae, the Cactaceae show eastern vs. western centres of distribution, and a paucity in Amazonia, but differently to the Bromeliaceae, the centre for the primitive (leafy) type is in eastern South America.

The ranges of Bromeliad genera look like a series of points of divergence, but with every range overlapping that of other genera of the subfamily. Thus, there is no disjunct genus within the Bromeliaceae comparable to Maschalocephallus of Rapateaceae (Smith, 1974).

At the specific level the same kind series of points of divergence within each genus and subgenus is encountered, and in addition, four extreme cases of disjunction: Pitcairnia feliciana from West Africa, separated from the rest of the genus by the Atlantic Ocean, Greigia berteroi and Ochagavia elegans, both endemic to the Juan Fernandez Island, and Tillandsia insularis on the Galapagos (Smith, 1974).

Smith (1974) also observed that large disjunctions by land are highly suspect, whether generic or specific, because of inadequacies of collections, especially of epiphytes. Taxa that appear at first sight to have a disjunction of over a thousand miles can subsequently present a dozen intermediate stations. At the other extreme are genera like Puya and Navia which present a series of micro-disjunctions, with different species endemic to individual mountain tops.

Martinelli & Vaz (1988) studied the patterns of geographical distributions for 37 taxa of Bromeliaceae which occur in the high montane grassland of southeastern Brazil, and found four basic patterns of distribution which agreed with Kubitzki (1975) with regards to the narrow endemic pattern found in Davilla and Hernandia.

In the most complete monograph of Bromeliaceae, Smith & Downs (1974, 1977, 1979) recognised 2255 taxa for the family within 46 genera: Pitcairnioideae with 678 taxa; Bromelioideae with 643 taxa and, Tillandsioideae with 934 taxa. More recently, Luther & Sieef (1992) published an list of valid binomials of Bromeliaceae, comprising 3059 taxa distributed within 54 genera. The subfamily Pitcairnioideae with 1005 taxa, Bromelioideae with 846 taxa, and Tillandsia with 1208 taxa. Based on Luther & Sieef (1992), we estimate 1089 taxa

(36%) are exclusive to Brazil, with a total of 789 taxa (72%) ocurring in the Atlantic Rainforest province, including six endemic genera.

Fontoura et al. (1991) presented a preliminary checklist of the Bromeliaceae which occur in Rio de Janeiro State, Brazil and they found 245 species (314 taxa) with 36% of these taxa endemic to the State, and 82% of the taxa studied were found occurring at the moist forest formation. These authors concluded that this region has the greatest generic diversity (18 out of 20 genera) and greatest degree of endemism.

1.9. PHYTOSOCIOLOGY

The main investigations of bromeliad phytosociology have been carried out by Pittendrigh (1948), Veloso (1952, 1953) and Aragão (1967). All agree that there is a definite and orderly vertical distribution of zonation of the species in the forest in response to light. More recently, Grubb et al. (1963) and Grubb & Whitmore (1966) compared montane and lowland rainforest in Ecuador in terms of floristic composition and climate. They observed 710 individuals per plot in the lowland forest, and, as many other authors have concluded, they proposed the alternate fog-bound and fog-free periods are important determinants of Bromeliaceae distribution.

Holdridge (1967) considered that epiphytes (including Bromeliaceae) "fill a definite niche and the filling of that niche helped to bring equilibrium to the forest". Any increase in dew condensation stimulates new growth in Bromeliaceae. Richards (1952) noted that bromeliads, with their remarkable water-holding ability, often act as epiphytic colonizers. Gilmartin (1964) analysed the data from various authors and concluded that an increase in altitude results in concomitant increase in the size and abundance of Bromeliaceae.

Veloso (1952) studied the presence, tolerance, volume of water in leaf-tanks and sociability of 54 taxa of Bromeliaceae in southeastern Brazil. He ranked all of the plants in terms of their humidity and light requirements. Of the 21 ciophiles, nine were "very humidity-demanding" and none of the shade-loving taxa grew under conditions of low humidity. He observed 13 species which were intermediate in their light requirements, only one of which was very demanding of humidity. Of the 42 species and 12 varieties observed, 19 of 20 taxa which were heliophiles were not humidity demanding. The bromeliad communities studied by Veloso & Klein (1957) had a much higher density than other workers have noted in other countries. They recorded 3.65 individual plant/m^2 whereas the highest density noted by Grubb et al. (1963) was 1.52 individuals/m^2.

Few attempts have been made to relate environmental parameters to the distribution of specific Bromeliad species. Relative humidity appears to be an important factor affecting many species. In the tropics many botanists have noted the extremely local distribution of some Bromeliaceae species. (Foster, 1943). There are many reports of species limited to a single mountain top, as in Fernseea itatiaiae, Vriesea altimontana, Vriesea farneyi, Vriesea pabstii, Tillandsia reclinata which are known from an area of less than one hectare (McWilliams, 1974; personal observation).

1.10. ASSOCIATED FAUNA

An extensive literature has developed on the animals which live in bromeliad leaf water-tanks and leaf bases. Picado (1913) listed 250 animal species which were found in such tanks. Wheeler (1942) reviewed much of the literature on the subject and produced an updated list of animals and noted that the list represented only a small fraction of the total Bromeliaceae fauna.

A number of workers (Dunn, 1937; Smith, 1941; Foster 1953; Neill, 1951; Laessle, 1961; Van Hyning, 1962; McWilliams, 1969; Benzing, 1970) have made significant additions to Wheeler's list. Almost all groups of animals that generally inhabit lakes and swamps have representatives in the Bromeliad leaf-tank fauna, and these are associated with an even greater number of other animals that are never present in terrestrial bodies of water but find favorable conditions of existence in the epiphytic bromeliads. A voluminous literature which developed in connection with malaria mosquito research indicates that there is an altitudinal zonation of mosquito species in the rainforest corresponding to that of Bromeliad habitats. (Smith, 1953; Klein, 1967; McWilliams, 1974).

McWilliams (1974) concluded that the Bromeliaceae offer a wealth of evolutionary and ecological problems to biology students, and that the obvious importance of natural selection in the family contrasts with the viewpoint that natural selection theory is not applicable to evolution of the family level. In particular there would seem to be numerous examples or coevolution between Bromeliaceae and animals in the water-tanks formed by the leaf sheaths.

CHAPTER 2. POLLINATION BIOLOGY AND BREEDING SYSTEMS IN BROMELIACEAE

2.1. POLLINATION AND FLORAL BIOLOGY

Surprisingly, for a family with many species with large attractive flowers, relatively little has been published on the pollination biology of Bromeliaceae. Certainly, very few species have been the object of detailed field studies. A list of published studies with putative pollinators and the authors is provided in the Table 2.1.1.

The earliest information on pollinators in the Bromeliaceae was presented by Knuth (1904), based mainly in the observations of Ule (1896, 1898, 1899), Johow (1898) and Müller (1896a, 1986b, 1897). Knuth listed bees, bumblebees, butterflies and hummingbirds which had been observed visiting bromeliad flowers.

Harms (1930) wrote a chapter on pollination in his monograph of the Bromeliaceae using some information largely derived from Knuth (1904), and he observed that the sticky and sculptured pollen, and often rich nectar secretion, indicated pollination by insects or birds but that the genus Navia seemed to be anemophilous. Harms (1930) suggested that many species of Pitcairnia are pollinated by butterflies or hummingbirds whereas bees, moths, bumblebees and small insects had a unclear role as important pollinators of Bromeliaceae.

Ruschi (1949) in a study of food plants and the re-introduction of some hummingbird species in southeastern Brazil, observed that in most cases where Bromeliaceae are pollinated by hummingbirds, the transport of the pollen is made by the head, beak and neck, deposited whilst the hummingbirds visit the flowers to find nectar at the base of corolla. This author suggested the name 'trochilogamy' for the pollination made exclusively by hummingbirds as distinguished from the more usual ornithophily, for flowers that are visited by birds but not necessarily pollinated by them.

The list of genera and species of Brazilian Bromeliaceae indicated by Ruschi (1949) as pollinated by hummingbirds is extensive (see Table 2.1.1). Unfortunately, Ruschi did not mention how his observations were made and some of his data seems to have been collected with cultivated plants, such as those for *Billbergia amoena* var. *amoena*, *Billbergia* sp., and *Vriesea carinata*.

In a later work, Ruschi (1982) studied the hummingbirds of Espírito Santo State, Brazil. He pointed out that hummingbirds play a effective role as pollinators of Bromeliaceae and he noted the preference that hummingbirds seem to have to visit plants of this family.

Wolf (1970) demonstrated the pollination of *Bromelia pinguin* by hummingbirds (Table 2.1.1) in a study on foraging behaviour and territoriality in hummingbirds of Costa Rica. McWilliams (1974) summarized the work of earlier authors such as Ule (1896), Knuth (1904), Werth (1915), Harms (1930), Skutch (1964), and Gilmartin (1969) among others, which noted that hummingbirds are the major pollinators of the Bromeliaceae. In his report to the monograph by Smith & Downs, McWilliams (1974) presented a Table which listed the birds which have been observed as Bromeliaceae pollinators. (Table 2.1.1).

As pointed out by McWilliams (1974), few authors have identified the specific birds or vectors. However, Johow (1898), Porsch (1932, 1935, 1936), Vogel (1969), Abendroth (1965) and Wolf (1970) and more recently Salas (1973), Sazima et al., (1989), Murawski & Hamrick, 1990 and Araujo et al., (unpublished data) made more precise observations and have commented on pollinator behavior, floral rewards, pollen transfer, fruit and seed set.

In a study of the causal factors in the temporal organization of blooming patterns of co-adapted group of plants sharing hummingbirds as their pollinator in Finca La Selva, Costa Rica, Stiles (1978) observed that *Aechmea mariae-reginae*, Aechmea nudicaulis, Guzmania monostachia, Guzmania lingulata var. minor (as ’G.minor’) and Guzmania scherzeriana (as ’G.scherziana’) were pollinated by hummingbirds and suggested that, in spite of the sparse observations, Aechmea mexicana, Tillandsia excelsa and Aechmea pubescens were possibly pollinated or at least occasionally used as foodplants, by hummingbirds. For Aechmea pubescens, Stiles (19878) suggested that despite visits by hummingbirds, this species was probably pollinated by butterflies and that Vriesea gladioliflora was probably pollinated by bats.

Sick (1984) in the chapter on the Trochilidae in his book on the birds of Brazil, observed that the Brazilian species of hummingbirds prefer flowers with dilute nectar, just a little higher than 20% of sucrose equivalent, in contrast to bees which prefer concentrations around 70%. This relationship between nectar concentration and vector type has been explored in some detail by Baker (1975) and Baker & Baker (1983). Sick (1984) observed that the colour of the flower and bracts, and in some cases the colour of the plant as a whole, is the main attraction to hummingbirds and that they can identify the changes in flower colours that signal the onset of nectar production, and that this change in colour is a common feature in Bromeliaceae. He also noted that quite small bromeliad species with insignificant flowers are also visited by hummingbirds, presumably on account of the ’learned’ nectar-reward, but that the most attractive bromeliad species for hummingbirds are the terrestrial and epiphytic species which have yellow or red flowers or bracts.

Utley (1983) in a systematic revision of the Middle American tecophylloid Vriesea (Xiphion), made observations on the possible pollinators of this group. This author found three different groups of species: those with day-blooming anthesis and pollinated by hummingbirds, species with crepuscular blooming which the author suggested were also pollinated primarily by hummingbirds, and those with nocturnal anthesis which he presumed to be pollinated by bats and 'night flying insects'. No detailed observations were made to confirm these hypotheses.

Murawski & Hamrick (1990) in a study of the genetic and clonal structure in a population of Aechmea magdalenae (see below) observed the main pollinator to be the hummingbird Phaetornis superciliosis, which is a known trapliner of understory plants. Araujo et al. (unpublished data), studied the flowering sequence and pollination of Vriesea carinata, Vriesea ensiformis and Vriesea incurvata, and noted that the hummingbird Ramphodon naevius was the only visitor of these species. These authors hypothesized that the different flowering phenologies observed in these three species were an adaptation to 'escape' from competition effects due to pollinator-sharing.

Bernardelo et al. (1991) studied the chemical composition and nectary structure of 20 taxa of Bromeliaceae (Table 2.1.1), belonging to eight genera from the three subfamilies. The nectar components reported by these authors were mostly new and they observed that hummingbirds constituted the main pollinator of the species studied, but they also observed butterflies and bees cropping nectar and pollen in few species.

Chiropterophily in Bromeliaceae has been reported for relatively few species by Porsch (1932, 1935, 1936), Vogel (1969), Salas (1973), Rauh (1986) and Sazima et al. (1989), (see Table 2.1.1).

Vogel (1969) provided evidence of pollination of Vriesea morrenii by the bat Anoura caudifer, and he listed species of the genus Vriesea section Xiphion, as showing a chiropterophilous syndrome. Rauh (1986, 1987) suggested bat pollination for Vriesea dressleri, Vriesea parvula and Vriesea patzeltii var. panamensis.

Salas (1973) proved that Vriesea nephrolepis (sensu Utley, 1983), is pollinated by the glossophagine bat Anoura geoffroyi, thus confirming the earlier prediction of Porsch (1932, 1935, 1936), that some Central American species of Vriesea (Xiphion) were pollinated by bats. Helversen & Helversen (1975 in: Dobat

& Peikert-Holle, 1985) cited in the work of Sazima et al. (1989) reported that individuals of the bats Anoura geoffroyi and Glossophaga soricina were kept alive in laboratory conditions in Germany where they fed on nectar of flowers of cultivated plants of Vriesea gladioliflora and Vriesea rugosa.

Chiropterophily in Bromeliaceae had been reported only for the subfamily Tillandsioideae (species of the genus Vriesea) until the work of Sazima et al. (1989) which demonstrated that the species Encholirium glaziovii was pollinated by the bat Lonchophylla bokermanni, and this constituted the first record chiropterophily for a member of subfamily Pitcairnioideae. The study by Sazima et al., (1989) gave details of visiting behaviour of the bat species and of the floral syndrome. They concluded that the greenish-yellow colouration, a wide-mouthed solid perigyn, rigid spreading stamens and style, copious thin nectar and musky flower odour which slightly increased at night, clearly characterized Encholirium glaziovii as adapted to pollination by bats.

Pollination by insects has been suggested to the Bromeliaceae family by some earlier authors such as Ule (1896, 1898), Müller (1896b, 1898), and Knuth (1904) and, recently, by Benzing (1980), Gardner (1986), Till (1992), and Varadarajan & Brown (1988), (Table 2.1.1), but none of these authors provided documentary evidence of such a pollination mechanism.

Varadarajan & Brown (1988) suggested that in the subfamily Pitcairnioideae the pollination syndromes for entomophily and chiropterophily are evident and that insect pollination may be widespread in genera such as Cottendorfia, Brocchinia, Deuterocohnia, Dyckia, Fosterella, among others. For these authors, entomophily was indicated in taxa with flowers which show a small stigma without papillae, diurnal anthesis, white, yellow, or green, actinomorphic flowers and with moderate amounts of nectar. These authors studied the anatomy/morphology of flowers and nectaries and linked this to observations on pollination type reported at second-hand by Proctor & Yeo (1973).

Harms (1930) was the first author to note that protandry seems to be common in the family, whilst fragrance was very not common, having only been observed up to that time in *Tillandsia xiphioides*, *T.fragrans*, *T.hamaleana*, *T.duratii*, *T.lanbeckii*, *Pitcairnia suaveolens*, *Streptocalyx floribundus*, *Hohembergia augusta*, *Aechmea cylindrata* and *Vriesea regina*.

In a comparison of the quantities of nectar produced in various species of Bromeliaceae, McWilliams (1974) agreed with Percival (1965) who had observed that, in general, angiosperm species with large flowers produce the greatest amounts of nectar, and he noted that Bromeliaceae are no exception to this 'rule', ranging in production from 160mg 'sucrose equivalents' in the floral exudate of the large-flowered *Pitcairnia macrochlamis*, to 3mg in the small-flowered *Aechmea fulgens*.

Percival (1965) noted that in many flowers, in diverse families, there is a remarkable parallelism between the level of the nectar in the floral tube and the length of the tongue of pollinators, and suggested that the major function of petal appendages in Bromeliaceae is perhaps in determining the height at which the nectar is held in the floral tube, which in turn influences the type of pollinators which can reach the nectar. The importance of the petal appendages of Bromeliaceae in pollination biology has been discussed by many authors but their specific role in relation to the floral biology and pollinators still remains to be determined.

Brown & Terry (1992), in a excellent anatomical and morphological study of the petal appendages in the Bromeliaceae and their significance in the taxonomy of the family, suggested that the petal appendages are most likely involved in intrafloral nectar management, such as nectar retention, presentation and delivery in accordance with the work of Böhme (1988) and Ueno (1989). These latter authors had demonstrated the location of duct and pore systems which are needed to deliver septal nectary products to the intrafloral chamber. Brown & Terry (1992) noted that different names had been applied to the same structure:

ligules, petal scales, petal appendages, nectariferous scales, lateral folds, vertical calli or callosities.

Utley (1983) and Brown & Terry (1992) also noted that the petal appendages loosely partition the intrafloral chamber into two sector which can be designated cappillary-space and non-capillary-space. In hypogynous flowers with petal appendages, the capillary-space or nectar chamber is located between the outer surface of ovary wall and the adaxial surfaces of the petal appendages and adjacent staminal filaments. The capillary-space in Bromelioideae flowers which have an inferior or semi-inferior ovary, is delineated by the inner hypanthium floor and wall, and the the petal appendages are involved in the retention of nectar, especially for horizontal to inclined flowers. Brown & Terry (1992) pointed out that the retention of a substantial volume of nectar per flower is consistent for taxa where the presumed pollinators are birds or bats, animals which have high energy requirements. These authors also proposed that other functions for Bromeliaceae petal appendages are possible, including tongue guides and protection against nectar dessication, but stated that demonstration of this will require a substantial effort.

Varadarajan & Brown (1988) looked at the significance for pollination biology of some morphological variations in petal scales, septal nectaries and stigmas of taxa of the subfamily Pitcairnioideae, and they concluded that the complexity of petal appendage morphology does not necessarily provide a reliable indication of nectar storage capacity, and that other aspects of floral structure may substitute for petal appendages to aid in the storage of the nectar, such as the coherent and swollen filaments bases of Dyckia.

Brown & Gilmartin (1988) in a study of the comparative ontogeny of the stigma in over 400 bromeliad taxa, suggested that the conduplicate-spiral stigma architecture has some selective advantages for ornithophily, since the three stylar lobes, twisted together, provided a greater stigmatic surface area and at the same time provided a rigid stylar support.

Brown & Gilmartin (1989) further surveyed stigma morphology in Bromeliaceae and found five morphological categories accounted for all known variations in stigma type. They speculated that the conduplicate-spiral, convolute-blade, and coralliform stigmas are morphological adaptations that increase stigmatic surface area, although both hummingbirds and bat visitation have been documented for Vriesea species which have the cupulate-type stigma, whilst taxa with simple-erect stigmas, as in the genus Tillandsia, appear to be pollinated by small moths as observed by Gardner (1986).

Gardner (1986) in a general review of pollination biology, studied 85 species of Tillandsia and found characteristics of assumed pollinating vector related to the floral architecture, flower and inflorescence pigmentation, and phenology, and she discussed the combinations of such characters which were correlated with the pollination biology and breeding systems. These views were based on long field experience, but apparently with no detailed studies of particular species. This author divided the Tillandsia species in five groups (Table 2.1.2) which, it was claimed, represent more natural assemblages than the present subgenera, since it separates the groups by floral character states.

In the group 1, Gardner (1986) listed 60 taxa (Table 2.1.2; see also Table 2.1.1) which are supposedly self-pollinated since the filaments often elongate after the anthers mature, until the anthers contact the stigma. For the taxa of this group, she suggested that the lack of specialization with regard to pollinators may be an important factor in the success of members of this group, and that the apparent lack of fragrance, even in nocturnal or crepuscular flowers, and the brightly coloured bracts of many species, suggest that ornithophily is the primitive pollination type for this group, despite the presence of a variety of adaptations that can be suitable to different pollinators.

For the 11 taxa of group 2, Gardner (1986) suggested that large moths are probably the specialized pollinators, since this group presents petal colours ranging from white, greenish-white to pale lavender, and no fragrance was detected.

For species of her group 3, Gardner (1986), had not made any field observations of pollinators, but rather she observed that examples of these species cultivated in gardens were visited by honeybees. She stated that species of this group are consistent with characteristics of 'bee-flowers' (Faegri & Pijl, 1979). For the groups 4 and 5, Gardner (1986) suggested that both are pollinated by small moths, due the pale flowers and vestite anthers. This author concluded that although hummingbirds may be important pollinators of Tillandsia species, characteristics of moth-syndrome were found in some members of each of the five groups examined, but that fragrance was observed in only one species.

Till (1992), in a study of the systematics and evolution of Tillandsia subgenus Diaphoranthema, distinguished six groups of species on the basis of floral morphology and certain vegetatives features. Till (1992) pointed out that in xeric species of subgenus Phytarrhiza the corollas are usually conspicuous, violet and fragrant, and that autogamy and cleistogamy had not been observed. In the species of Tillandsia subgenus Diaphoranthema, Till (1992) observed that the attractive function of the petals is of little importance, since the petals are reduced in size and strongly narrowed and the prevailing colours are yellowish and brown. Floral fragrance occurs in some species, and it was surmised that pollinator attraction is probably effected by floral fragrance in several allogamous species. However, some species of this subgenus do have fragrant flowers with open corollas with spreading petal lobes, which, contrary to all expectations, are autogamous. Several species are autogamous or even cleistogamous and the anthers are often in close contact with the stigma and form a hood above it which prevents cross-pollination. Till (1992) concluded that the flowers of xeric species of Tillandsia subgenus Phytarrhiza appear to be attractive to insects and although they have a very narrow throat, they have a distinct floral fragrance, and were considered to be entomophilous. The usually violet petals are in accord with diurnal insect

(Hymenoptera) visits/pollinations, as had been observed in Tillandsia purpurea in coastal desert of Peru. In these species, the enclosed anthers are located above the stigma and are not in contact with it, and the sticky pollen rarely seems to drop onto the receptive surface of the stigma in the same flower.

In the highly neotenous group of species within Tillandsia subgenus Diaphoranthema, Till (1992) observed a characteristic reduced size of the vegetative body and depauperate inflorescences which are frquently one-flowered. Such species rapidly reach reproductive age and behaving like "island floras", with high degree of polyploidy, and Till (loc. cit.) hypothesized that the stimulus for the evolution of neotenous forms in subgenus Diaphoranthema could have been the climatic changes during the Pleistocene, which caused the development of features to permit survival in the increased dry habitats, and that subsequently these features were an advantage for occupying new ecological niches.

Evans & Brown (1989) studied the plicate staminal filaments in Tillandsia subgenus Anoplophytum from a morphological and anatomical viewpoint, and they hypothesized that a possible functional significance of plicate filaments is that collectively they may form a plug-like barrier within the floral tube and this may retard evaporation of nectar as well as serving as a mechanism to draw dehiscent anthers back to the level of the stigma as a tardy self-pollination mechanism. These authors stated that the manifestation of filament- plication at mid- to late-anthesis is consistent with this view, despite the fact that the positional relationships between the anthers and stigma throughout anthesis do not support this hypothesis.

2.2. BREEDING SYSTEMS

Since the observations of Harms (1930) very little has been published on the breeding systems of Bromeliaceae species. Table 2.2 lists the probable breeding systems for Bromeliaceae taxa as reported in the literature, adapted from

Table 2.1.1. Taxa of Bromeliaceae and putative pollinators, visitors, pollination types as cited by the authors.

Aechmea bromeliifolia	hummingbirds	Knuth (1904)
A. caudata	hummingbirds	Ruschi (1949)
A. coelestis	hummingbirds	Ruschi (1949)
A. distichantha	ornithophilous	Bernardello & al. (1991)
A. lamarchei	hummingbirds	Ruschi (1949)
A. lingulata	hummingbirds	Ruschi (1949)
A. magdalenae	*Phaetornis superciliosis*	Murawski & Hamrick (1990)*
	hummingbirds	Stiles (1978)
A. mariae-reginae	hummingbirds	Stiles (1978); Stiles & Freeman (1993)
A. mexicana	hummingbirds	Stiles (1978)
A. nudicaulis	hummingbirds	Ruschi (1949); Stiles (1978)
A. nudicaulis var. aureo-rosea	hummingbirds	Ule (1898)
	bees	Ule (1898)
A. organensis	hummingbirds	Ruschi (1949)
A. pineliana	hummingbirds	Ule (1896); Ruschi (1949)
	butterflies	Ule (1896)
A. pubescens	hummingbirds	Stiles (1978)
	butterflies	Stiles (1978)
A. purpureo-rosea	bees	Benzing (1980)
A. ramosa	hummingbirds	Ruschi (1949)
A. recurvata var. ortgiesii	hummingbirds	Ule(1898)
A. sphaerocephala	wasp (*Ageronia*)	Knuth (1904)
	mouths	Knuth (1904)
	bee	Knuth (1904)
	hummingbirds	Ruschi (1949)
A. triticina	hummingbirds	Ruschi (1949)
Ananas bracteatus var. bracteatus	*Euglossa nigrita*	Scrottky (1901)
A. comosus 'cultivars'	honeybees	Brewbaker & Gorrez (1967)
	beetle (Nitidulidae)	Brewbaker & Gorrez (1967)
Ayensua uiapanensis	chiropterophily	Varadarajan & Brown (1967)
Billbergia amoena var.amoena	*Clytolaema rubricauda*	Ruschi (1949)
B. amoena var.viridis	hummingbirds	Ruschi (1949)
B. elegans	hummingbirds	Knuth (1904)
B. euphemiae	hummingbirds	Ruschi (1949)
B. horrida	hummingbirds	Ruschi (1949)
	bees	Benzing (1980)
B. iridifolia	hummingbirds	Ruschi (1949)
B. magnifica	hummingbirds	Ruschi (1949)
B. morelli	hummingbirds	Ule (1896); Ruschi (1949)
B. porteana	hummingbirds	Ruschi (1949)

Table 2.1.1. Cont.

B. pyramidalis	hummingbirds	Knuth (1904); Ruschi (1949)
	ornithophily	Benzing (1980)
	Eupetomena macroura	Abendroth (1965)*
B. reichardtii	hummingbirds	Ruschi (1949)
B. sanderiana	hummingbirds	Ruschi (1949)
	Eupetomena macroura	Abendroth (1965)*
B. tweediana	hummingbirds	Ruschi (1949)
B. vittata	hummingbirds	Ruschi (1949)
Brocchinia steyermarkii	entomophily	Varadarajan & Brown (1988)
Bromelia binotii	hummingbirds	Ruschi (1949)
B. laciniosa	hummingbirds	Ruschi (1949)
B. pinguin	*Amazilia saucerottei*	Wolf (1970)*
	Amazilia rutila	Wolf (1970)*
	Phaeochroa cuvierii	Wolf (1970)*
	Heliomaster constantii	Wolf (1970)*
	Amazilia tzacatl	Wolf (1970)*
	Chlorostilbon canivetii	Wolf (1970)*
	Phaetornis longuemareus	Wolf (1970)*
Canistrum auranthiacum	hummingbirds	Ule (1898)
Catopsis nutans	bees	Benzing (1980)
Deuterocohnia haumanii	ornithophily	Bernardello & al. (1991)
D. longipetala	entomophily	Varadarajan & Brown (1988)
	Chlorostilbon aureoventris	Bernardello & al.(1991)*
D. schreiteri	entomophily	Varadarajan & Brown (1988)
Dyckia ferox	ornithophily	Bernardello & al. (1991)
D. floribunda	*Chlorostilbon aureoventris*	Bernardello & al. (1991)*
	Sappho spargamura	
	Papilio thoas	
Dyckia hilaireana	*Augastes scutatus*	Sazima & al. (1989)
D. ragonesei	*Chlorostilbon aureoventris*	Bernardello & al. (1991)*
D. aff. tuberosa	ornitophily	Sazima & al. (1989)
Encholirium glaziovii	*Lonchophylla bokermanni*	Sazima & al. (1989)*
E. vogelii	bat	Sazima & al. (1989)
Fascicularia bicolor	hummingbirds	Mez (1896)
F. litoralis	hummingbirds	Mez (1896)
Greigia sphacelata	hummingbirds	Johow (1898)

Table 2.1.1. Cont.

Guzmania lingulata var.minor	hummingbirds	Stiles (1978)
G. monostachia	hummingbirds	Stiles (1978)
G. scherzeriana	hummingbirds	Stiles (1978)
Hohembergia augusta	wasp (Zygaenidae)	Ule (1898)
	Apis melifera	Ule (1898)
	Trigona	Ule (1898)
	Augochlora	Ule (1898)
	flies	Ule (1898)
	hummingbirds	Ruschi (1949)
H. blanchetii	hummingbirds	Ruschi (1949)
Neoregelia ampullacea	hummingbirds	Ule (1896)
N. compacta	bees	Ule (1896)
	hummingbirds	Knuth (1904)
N. sarmentosa	hummingbirds	Abendroth (1965)
Nidularium burchelii	bees	Ule (1896)
N. longiflorum	hummingbirds	Ule (1896)
N. microps var. microps	hummingbirds	Ule (1896)
N. procerum	hummingbirds	Ruschi (1949)
N. purpureum	hummingbirds	Ruschi (1949)
N. regelioides	hummingbirds	Ruschi (1949)
N. scheremetiewii	hummingbirds	Ruschi (1949)
Ochagavia elegans	hummingbirds	Knuth (1904)
Pitcairnia albiflos	hummingbirds	Ruschi (1949)
P. beycalena	hummingbirds	Ruschi (1949)
P. brevicalycina	entomophily	Varadarajan & Brown (1988)
Pitcairnia brittoniana	hummingbirds	Stiles & Freeman (1993)
P. bromeliifolia	hummingbirds	Ruschi (1949); Read (1969)
P. carinata	hummingbirds	Ruschi (1949)
P. corallina	ornithophily	Varadarajan & Brown (1988)
P. flammea	hummingbirds	Ruschi (1949)
P. lancifolia	hummingbirds	Ruschi (1949)
P. loki-schmidtii	chiropterophily	Vogel (1969)
P. macrochlamys	moths	Benzing (1980)
P. meridensis	ornithophily	Varadarajan & Brown (1988)
P. nubigena	ornithophily	Varadarajan & Brown (1988)
P. staminea	hummingbirds	Ruschi (1949)
P. undulata	ornithophily	Benzing (1980)

Table 2.1.1. Cont.

Portea petropolitana	bees	Ule (1896)
	hummingbirds	Ruschi (1949)
Pseudoananas sagenarius	bees (*Trigona*)	Muller (1896)
Puya alpestris	hummingbirds	Johow (1898)*
P. aristeguietae	chiropterophily	Varadarajan & Brown (1988)
P. chilensis	*Mimus tenca*	Werth (1915)*; Knuth (1904)
	Curaeus aterrimus	Johow (1898)*; Knuth (1904) Harms (1930)
	Turdus megellanicus	Johow (1898)*; Knuth (1904)
	Patagonia gigas	Johow (1898)*; Knuth (1904)
P. coerulea	*Curaeus aterrimus*	Johow* (1898); Knuth (1904)
P. ferruginea	chiropterophily	Vogel (1969)
P. mirabilis	chiropterophily	Vogel (1969)
P.spathacea	*Chlorostilbon aureoventris*	Bernardello & al. (1991)*
P. venusta	hummingbirds	Johow (1898); Knuth (1904)
Quesnelia arvensis	moths	Ule (1896)
	large bees	Ule (1896)
	hummingbirds	Ule (1896)
Q. liboniana	hummingbirds	Knuth (1904)
Streptocalyx floribundus	hummingbirds	Ule (1898)
Tillandsia aeris-incola	entomophily	Ule (1900)
T. albertiana	ornithophily	Benzing (1980)
T. albida	small moths	Gardner (1986)
T. andreana	ornithophily	Benzing (1980)
T. argentea	small moths	Gardner (1986)
T. dasyliriifolia	small moths	Gardner (1986)
T. deppeana	honeybees	Gardner (1986)
T. dugesii	hummingbirds	Gardner (1986)
T. duratii	bees	Benzing (1980)
	psychophily	Bernardello & al. (1991)
T. ehrenbergii	small moths	Gardner (1986)
T. excelsa	hummingbirds	Stile (1978)
T. filifolia	small moths	Gardner (1986)
T. flexuosa	small moths	Gardner (1986)
T. gardnerii	hummingbirds	Ruschi (1949)
	Phaetornis eurynome	Abendroth (1965)*
T. geminiflora	hummingbirds	Ruschi (1949)
T. heterophilla	small moths	Gardner (1986)
T. ignesiae	small moths	Gardner (1986)
T. imperialis	honeybees	Gardner (1986)
	ornithophily	Benzing (1980)
T.karwinskyana	small moths	Gardner (1986)

Table 2.1.1. Cont.

T. kegeliana	small moths	Gardner (1986)
T. lampropoda	bees	Gardner (1986)
T. lepidosepala	small moths	Gardner (1986)
T. limbata	small moths	Gardner (1986)
T.lorentziana	*Chlorostilbon aureoventris*	Bernardello & al. (1991)*
T. makoyana	small moths	Gardner (1986)
T. plumosa	small moths	Gardner (1986)
T. ponderosa	honeybees	Gardner (1986)
	large bees	Gardner (1986)
T. propagulifera	small moths	Gardner (1986)
T. socialis	small moths	Gardner (1986)
T. streptocarpa	bees	Benzing (1980)
T. streptophylla	hummingbirds	Gardner (1986)
T. usneoides	moths	Benzing (1980)
T. utriculata	hummingbirds	Gardner (1986)
	small moths	Gardner (1986)
T. xiphioides	sphingophily	Bernardello & al. (1991)
Vriesea altodaserrae	ornithophily	Vogel (1969)
V. amethistina	hummingbirds	Ruschi (1949)
V. atra	chiropterophily	Vogel (1969)
V. balanophora	hummingbirds	Utley (1983)
V. bituminosa	chiropterophily	Vogel (1969)
V. carinata	hummingbirds	Porsch (1924); Ruschi (1949); Abendroth (1965)
	Ramphodon naevius	Araujo & al. (unpub. data)*
V. chrysostachys	ornithophily	Vogel (1969)
V. corcovadensis	hummingbirds	Muller (1897); Ruschi (1949)
V. densiflora	ornithophily	Vogel (1969)
V. dressleri	chiropterophily	Rauh (1986)
V. ensiformis var. ensiformis	hummingbirds	Muller (1896); Ruschi (1949)
	Ramphodon naevius	Araujo & al. (unpub.data)*
V. erythrodactylon	hummingbirds	Ruschi (1949)
V. fenestralis	chiropterophily	Vogel (1969)
V.friburgensis	*Colibri conruscan*	Bernardello & al. (1991)*
V. geniculata	bee	Ule (1898); Knuth (1904)
	Sphingidae	Porsch (1924)
V. gladioliflora	chiropterophily	Vogel (1969)
	Anoura geoffroyi	Herversen & Herversen (1975)
	Glossophaga soricina	Herversen & Herversen (1975)
V. goniorachis	chiropterophily	Vogel (1969)
V. hainesiorum	ornithophily	Utley (1983)
V. heterostachys	hummingbirds	Abendroth (1965)
V. hieroglyphica	hummingbirds	Ruschi (1949)
	chiropterophily	Vogel (1969)
V. incurvata	*Ranphodon naevius*	Araujo & al. (unpub.data)*
V. inflata	hummingbirds	Ruschi (1949)
V. irazuensis	*Anoura geoffroyi*	Salas (1973)*
	ornithophily	Utley (1983)
V. itatiaiae	chiropterophily	Vogel (1969)

Table 2.1.1. Cont.

V. jongheii	hummingbirds	Muller (1897); Knuth (1904) Ruschi (1949)
	chiropterophily	Vogel (1949)
V. latissima	bats	DeVries (date?)
V. leucophylla	hummingbirds	Utley (1983)
V. longicaulis	hummingbirds	Ruschi (1949)
	chiropterophily	Vogel (1969)
V. lubersii	hummingbirds	Abendroth (1965)
V. luis-gomezii	hummingbirds	Utley (1983)
V. lyman-smithii	bats	Utley (1983)
	hummingbirds	Utley (1983)
V. macrostachya	chiropterophily	Vogel (1969)
V. modesta	hummingbirds	Ruschi (1949)
V. morrenii	hummingbirds	Ruschi (1949)
	Anoura caudifer	Vogel (1969)*
V. ororiensis	*Panterpe insignis*	Utley (1983)*
V. parvula	chiropterophily	Rauh (1986)
V. pedicellata	chiropterophily	Utley (1983)
V. picta	chiropterophily	Utley (1983)
V. philippocoburgii	ornithophily	Muller (1896); Vogel (1969)
V. platynema	*Anoura caudifer*	Herversen & Herversen (1975)
V. poenulata	hummingbirds	Ruschi (1949)
V. procera var. procera	hummingbirds	Ruschi (1949)
V. psittacina var.psittacina	hummingbirds	Ruschi (1949)
V. ptzeltii var. panamensis	chiropterophily	Rauh (1986)
V. regina	chiropterophily	Vogel (1969)
V. regnellii	chiropterophily	Vogel (1969)
V. rugosa	*Anoura geofroyi*	Herversen & Herversen (1975)
	Glossophaga soricina	Herversen & Herversen (1975)
V. scalaris	hummingbirds	Muller (1897); Ruschi (1949)
V. sceptrum	ornithophily	Vogel (1969)
V. simplex	hummingbirds	Ruschi (1949)
V. stenophylla	chiropterophily	Utley (1983)
V.thyrsoideae	ornithophily	Vogel (1969)
V. umbrosa	nocturnal insects	Utley (1983)
V. unilateralis	hummingbirds	Ruschi (1949)
	chiropterophily	Vogel (1969)
V. uxoris	hummingbirds	Utley (1983)
V. viridiflora	chiropterophily	Vogel (1969)
V. viridis	hummingbirds	Utley (1983)
V. wawraneana	chiropterophily	Vogel (1969)
V. williamsii	chiropterophily	Utley (1969)

Obs. : This table records all indications concerning pollinators, visitors, and syndromes of pollination of Bromeliaceae species which have been found in the literature. Some reports are based on superficial observation of visitors to flowers of various species in the field whilst others are simply speculative comments based on the floral morphology of cultivated taxa. Data derived from detailed field observations are indicated with (*).

McWilliams (1974). Many published reports are speculative, and based on observations of floral structure, rather than being derived from studies involving controlled pollination experiments.

The occurrence of self-pollination in the Bromeliaceae was first suggested by Ule (1896, 1898) with his description of cleistogamous flowers in some Brazilian species of three genera of subfamily Bromelioideae: *Aechmea*, *Nidularium* and *Quesnelia*. However, Gilmartin & Brown (1985) have proposed that these "closed" flowers are in fact cross-pollinated by insects which invade the floral tissue and thus do not represent cleistogamy. But these later authors' did not provided details of cross-pollination in Ule's species.

Andromonoecy in Bromeliaceae is known only in a few species of *Cryptanthus* (Smith, 1955; Brown & Gilmartin, 1989; personal observation), and dioecy is found in the xerophytic genus *Hechtia*, with 49 species completely dioecious, and in *Catopsis*, with 19 species ranging from fully dioecious to those with hermaphrodite flowers (Brown & Gilmartin, 1989). Varadarajan (1986) found a rare case of unisexual flowers in *Dyckia*.

Cleistogamy is considered a derived system in Bromeliaceae by Brown & Gilmartin (1989) and has been documented for *Tillandsia variabilis* (Gardner, 1986) and *Tillandsia capillaris* by Gilmartin & Brown (1985) who found this species growing epiphytically, with closed, self-pollinated flowers. These authors noted that chasmogamous flowers have the gynoecium and androecium tighly enclosed inside the perianth. The six anthers were clustered around the minute three-lobed, simple-erect stigma and remain in close association with the stigma at least through capsule elongation. They observed that there is no apparent anther dehiscence in the cleistogamous flowers of *Tillandsia capillaris*, contrasting to anthers of the chasmogamous flowers which dehisce longitudinally, and noted that the seeds from boths types of flowers appear normal. Those authors did not present data with regard to differences in either seed number or germinability, or

Table 2.1.2. The five groups of Tillandsia subgenera Tillandsia and Allardtia, by natural assemblages of floral character states, as suggested by Gardner (1986).

Group I:
T.achyrostachys
T.acostae
T.aguascalientensis
T.andrieuxii
T.bauleyi
T.bartramii
T.bourgeae
T.brachycaulos
T.buchii
T.bulbosa
T.butzii
T.califanii
T.calothyrsus
T.caput-medusae
T.carlsoniae
T.chaetophylla
T.chiapensis
T.chlorophylla
T.circinnatoides
T.compressa
T.concolor
T.cossonii
T.dugesii
T.eizii
T.erubescens
T.fasciculata
T.festucoides
T.flabellata
T.ionantha
T.ionantha v. vanhyningii
T.jaliscomontecola
T.juncea
T.kalmbacherii
T.kirchoffiana
T.macdougallii
T.magnusiana
T.matudae
T.mazatlanensis
T.orogenes
T.ortgieseana
T.parryi
T.aff. parryi
T.paucifolia
T.polystachia
T.prodigiosa
T.pseudobaileyi
T.punctulata
T.rodrigueziana
T.roland-gosselinii
T.rotundata
T.schiedeana
T.schiedeana v. glabrior
T.seleriana
T.setacea
T.simulata
T.streptophylla
T.tricolor
T.vicentina var. glabra
T.violacea
T.xerographica

Group II:
T.albida
T.argentea
T.dasylirifolia
T.flexuosa
T.karwinskyana
T.kegliana
T.limbata
T.makoyana
T.propagulifera
T.socialis
T.utriculata

Group III:
T.deppeana
T.heterophylla
T.imperialis
T.lampropoda
T.lauii
T.multicaulis
T.ponderosa
T.yunckerii

Group IV:
T.filifolia

Group V:
T.ehrenbergii
T.ignesiae
T.lepidosepala
T.plumosa

how the pollen grains germinated and pollen tubes reach the ovules, in the cleistogamous flowers since that the anthers apparently do not open.

Read (1969) in a study on Pitcairnia bromeliifolia suggested this species was self-compatible due to the fact that the petals twist together bringing the anthers and stigma into close contact following anthesis, although the author did not test for self-compatibility in his study.

McWilliams (1974) suggested that species of Tillandsia subgenus Tillandsia, such as Tillandsia juncea, T. fasciculata, T. tricolor, T. butzii, T. caput-medusae and T. schiedeana are self-fertile, whilst many Guzmania and Vriesea species, including Vriesea splendens are self-pollinated. For the subfamily Bromelioideae, this author suggested that Aechmea angustifolia, A. bromeliifolia and A. mexicana are examples of self-pollinated species, whereas Aechmea fulgens and A. nudicaulis do not appear to be self-pollinated. Also according to McWilliams (1974) most species of Billbergia subgenus Helicoidea appear to be inbreeders although species of subgenus Billbergia, the most primitive group, are primarily outcrossers. In the Pitcairnioideae, McWilliams (1974) suggested that Pitcairnia andreana, P. xanthocalyx and Puya mirabilis are some examples of inbreeders, and he concluded that a detailed study of breeding systems in Bromeliaceae would be likely to have both systematic and ecological implications, and he agreed with Mosquin (1966) that inbreeders apparently rarely gave rise to outbreeders. McWilliams (1974) did not mention what kind of experiments were undertaken to establish the types of breeding systems proposed for these diverse taxa.

Gardner (1986) suggested that Tillandsia punctulata is out-crossing whilst Tillandsia variabilis is self-pollinated with cleistogamous flowers.

The great abundance of artifical hybrids produced by horticulturists attest to the fact that interspecific incompatibility may be of minor importance in isolating species under natural conditions but natural hybrids appear to be rare under field conditions (Smith, 1955; Collins & Kerns, 1958; McWilliams, 1968).

McWilliams (1974) observed that the majority of the Tillandsioideae of Florida - USA are self-pollinated, and he suggested that Mosquin's (1966) hypothesis that reproductive specialization such as selfing, which promotes genetic uniformity in such populations, may be critical for the adaptation and evolution of plants to colder climates may be applicable to such bromeliads. Hall (1958) observed that for the Bromeliaceae, Florida has a cool climate, and from time to time there occur severe frosts, as a consequence of which large numbers of native Bromeliaceae are killed.

Garth (1964) studied the ecology of Tillandsia usneoides and pointed out that in a experiment with 30 flowers collected from plants monitored under natural conditions, all but four had pollen grains on the stigma. Five of these had pollen tubes penetrating the style. In his experiment, this author bagged 8 flowers and 4 were examined after the flower had wilted and found that none showed developing pollen tubes, but all had self-pollen on the stigma. Of the four which were not touched for 3 months, one developed an aborted capsule and the others rotted at an early stage and no pollinator vector was noted despite continued observations.

Dodson & Gillespie (1967) studied orchid species which also cross freely, and concluded that mechanical and ethological isolation were the critical factors which prevented hybridization between otherwise compatible taxa. Benzing (1980) suggested that Tillandsia subgenus Tillandsia in Mexico seems to be an exception, and that some species of this group present frequent interspecific hybrids.

Brewbaker & Gorrez (1967) studied genetic segregation for self-incompatibility in clones of Ananas comosus cultivars and found that this species is highly self-incompatible. The results presented by these authors showed that in 450 crosses involving 20 progeny of A (female) x C (male), two intra-sterile, inter-fertile groups of 13 and 7 plants were obtained in the F1 family, and one of this group was cross-incompatible with the male parent (clone C). The results progeny tests of 331 crosses of C (female) x F (male), resulted that C x F cross were of the classical homomorphic gametophytic *S* allele type incompatibility. Brewbaker & Gorrez (1967) demonstrated that in preliminary studies of the inheritance of self-fertility in Ananas, the species A. comosus is the only SI species in the genus, while A. ananassoides, A. bracteatus are fully self-fertile, as is Pseudananas sagenarius. This study confirmed the theory that self-fertility is based on an *Sf* alleles of the *S* locus, since in selfs and test-crosses of five F1 hybrids of A. comosus x A. ananassoides, self-incompatible segregants were recovered with a high frequency from back-crosses to A. comosus. These authors also noted that seediness in pineapple, is more common in breeding nurseries than in commercial fields and that such sporadic cross-pollination appears to be the result of honeybee activity, although the pineapple beetle (Nitidulidae) has also been implicated.

Murawski & Hamrick (1990) studied the genetic and clonal structure of Aechmea magdalenae on Barro Colorado Island using isozymes markers, and found a substantial heterogeneity in allele frequencies. They pointed out that this value is high when compared to other species which shared the same suite of traits: monocots, tropical plants, long-lived perennials, plants with sexual and asexual reproduction, and outcrossing plants with seed dispersed by animal vectors. These authors observed that the flowers of Aechmea magdalenae are bisexual and produced few inflorecences during the period of three years' observation in comparison with the number of individuals, whilst the main pollinator is a hummingbird Phaetornis superciliosis, a known trapliner pollinator of many understory plants. Murawski & Hamrick (1990) suggested that the pollen flow between the disjunct patches of Aechmea magdalenae is relatively low due to the distances between such patches, and that this species seems to be genetically self-compatible, with the smaller populations probably exhibiting more selfing than larger populations by virtue of the limited opportunities for outcrossing during any flowering season. They concluded that the relationship with distance of samples sharing identical genotypes indicates that clones are local, with rosettes generally occurring within 10m of each other, but since even the smallest population studied consisted of multiple genotypes, this indicated either that populations are established by more than one seed, or that sexually derived individuals had become established after colonization. Although these authors suggested that this species is self-compatible, no controlled pollination experiments were carried out to determine the breeding system.

TABLE 2.2. Taxa of Bromeliaceae and putative breeding systems as cited by the authors.

Aechmea angustifolia	self-pollination	McWilliams (1974)
Aec. bromeliifolia	self-pollination	McWilliams (1974)
Aec. fulgens	cross-pollination	McWilliams (1974)
Aec. magdalenae	self-compatibility	Murawski & Hamrick(1990)
Aec. mexicana	self-pollination	McWilliams (1974)
Aec. nudicaulis	cross-pollination	McWilliams (1974)
Ananas ananassoides	self-fertile	Brewbaker & Gorrez(1967)
An. bracteatus	self-fertile	Brewbaker & Gorrez(1967)
An. comosus	self-incompatibility	Brewbaker & Gorrez(1967)
Billbergia subgenus Helicoidea	inbreeding	McWilliams (1974)
Billbergia subgenus Billbergia	outcrossing	McWilliams (1974)
Catopsis (partially)	dioecy	Brown & Gilmartin (1989)
Cryptanthus spp.	andromonoecy	Smith(1955);Brown&Gilmartin (1989)
Dyckia sp.	unisexual flowers	Varadarajan (1986)
Guzmania spp.	self-pollination	McWilliams (1974)
Hechtia spp.	dioecy	Brown & Gilmartin (1989)
Pitcairnia andreana	inbreeding	McWilliams (1974)
Pit. bromeliifolia	self-compatible	Read (1969)
Pit. xanthocalyx	inbreeding	McWilliams (1974)
Pseudananas sagenarius	self-fertile	Brewbaker & Gorrez(1967)
Puya mirabilis	inbreeding	McWilliams (1974)
Quesnelia spp.	self-pollination	Ule (1898)
Tillandsia butzii	self-fertile	McWilliams (1974)
T. capillaris	self-pollination	Gilmartin & Brown(1974)
T. caput-medusae	self-fertile	McWilliams (1974)
T. fasciculata	self-fertile	McWilliams (1974)
T. ionantha var. ionantha	out-crossing	Soltis & al. (1987)
T. juncea	self-fertile	McWilliams (1974)
T. punctulata	out-crossing	Gardner (1986)
T. recurvata	inbreeding	Soltis & al. (1987)
T. schiedeana	self-fertile	McWilliams (1974)
T. tricolor	self-fertile	McWilliams (1974)
T. usneoides	self-incompatibility	Garth (1964)
T. variabilis	self-pollinated	Gardner (1986)
Vriesea carinata	auto-incompatible	Araujo & al. (unpub. data)
Vriesea ensiformis	auto-compatible	Araujo & al. (unpub. data)
Vriesea splendens	self-pollination	McWilliams (1974)

CHAPTER 3. ATLANTIC RAINFOREST

3.1. INTRODUCTION

Brazil has the world's largest area of tropical forest, with an estimated total forested area of c. 3,600,000 km^2 (FAO/UNEP, 1981; IUCN, 1988). The greatest extent of Brazil's tropical forest occurs in the Amazonian region, which covers 42% of the country and with c. 80% of the Amazonian forest consisting of lowland moist forest formation. In contrast, in the densely populated Atlantic coastal area in eastern region, and in the agriculturally exploited interior, only fragments of forest still survive.

The Atlantic Rainforest province in Brazil originally covered for c. 1,4 million km^2, with a depth from the coast of 100 - 280 km. Within this band, the original formations and respective types of vegetation are now found in scattered remnants.

In a broad morphoclimatic, floristic and phytogeographical context, the Atlantic Rainforest province in Brazil includes several unique tropical and subtropical forest and non-forest formations, involving a complex of vegetation types and communities, which are largely distinct from the much more extensive Amazonian Rainforest province. Since the pioneer phytogeographical divisions for Brazil by Martius (1906), the limits of the Atlantic rainforest province have varied considerably according to various authors e.g. Sampaio (1945), Aubreville (1961), Hueck (1972), Romariz (1974), Rizzini (1976), Ferri (1980), UNESCO (1981), Eiten (1983) and Mori (1989).

In addition to the divergences between authors with regard to the limits and the phytogeographical nomenclature of the Atlantic forests, differences also exist with regard to the present state of botanical exploration, and floristic and phytosociological inventories. Also, some of the vegetation types have been disturbed and almost eliminated by man, as pointed out by Mori (1989).

Andrade-Lima (1953, 1977, 1981), Prance (1979), Gentry (1979), Mori et al. (1981), among other authors, have drawn attention to a number of species which have disjunct distributions between the Amazonian Rainforest and the Atlantic Rainforest provinces, and Ab'Saber (1972) with geomorphological data, Bigarella (1964) and Bigarella et al. (1975) with paleoclimatological data, have indicated that these two areas may have been linked until the expansion of seasonal forest occurred during the Pleistocene cool periods (Brown & Ab'Saber, 1979).

Coffee plantations and timber extraction, especially the most valuable timber species such as Cariniana legalis, Cariniana estrellensis, Dalbergia nigra, Cedrela fissilis, Caesalpinia echinata, Mezilaurus navalium has resulted in the relative rarity of such species today. Extraction of firewood and the production of charcoal has also been a constant factor in the forest since the colonization of Brazil. According to Dean (1985), household firewood consumption in southeastern region of Brazil at the turn of the century amounted to about 2m^3 per capita. Adding industrial uses to this raises the figure of 2,3m^3 of forest per year to supply the city of Rio de Janeiro, where 10,000 persons made their living by woodcuting and charcoal preparation (Mori, 1989).

The first massive deforestation in southeastern Brazil was caused by the sugar cane plantations which were introduced to São Paulo in 1531 or possibly even earlier (Dean, 1983). Rio de Janeiro State was one of the most important centers of production of sugar cane (Sick & Teixeira, 1979) and in 1709, Rio de Janeiro was exporting about 5,000 tons a year, about 20% of colony's total (Dean, 1983). Today the region of Campos, in the north of Rio de Janeiro State is the most important area of sugar plantation in the State, and in the past this area was occupied by extensive lowland wet forests.

Cattle raising has also been responsible for the destruction of large areas of moist forest and mesophytic forest formations, as in the areas located in the Paraiba River valley, and the north and northwest of Rio de Janeiro State, and in nearly all of the interior of São Paulo and Espírito Santo.

For the purpose of the present study, in order to characterize the Atlantic Rainforest province, I used as a base, the map of vegetation of IBGE (1989) and the atlas of forest remnants of the Atlantic rainforest domain (S.O.S. Mata Atlantica/IBAMA/INPE, 1990), revised by the participants of the Brazilian National Meeting on the Protection of Natural Ecosystems of the Atlantic Rainforest (S.O.S. Mata Atlantica, 1990), together with my personal observations.

On this view, the Atlantic Rainforest province includes the moist forest formations that present different types of forests and non-forests vegetation, according to the sector and region that are placed on the coastal plain and sea-ward slopes of the mountain chains, some mesophytic forest formations, with deciduous and semi-deciduous forest vegetation, 'restingas' formation and mangrove formation (Figure 3.1). The classification was based on the floristic composition and physiognomy in which 'formation' has a floristic and physiognomic connotation, together with climatic and topographic aspects, although many communities must be expected to show characteristics intermediate between two formations (Whittaker, 1980).

The differences between the types of forest of moist and mesophytic formation are still need of study and the data to separate some of them are not available. Some inventories carried out in mesophytic forests (Gibbs et al., 1980; Assumpção et al., 1982) and in moist forest formations (Soares & Ascoly, 1979; Pagano & Leitão Filho, 1987; Guedes, 1989; PMA, 1990, 1991, 1992) among others, have indicated floristic similarities with regard to some tree species.

Figure 3.1. Atlantic Rainforest province: sectors and centres of endemism.

Traditionally the Atlantic Rainforest extension has been divided into three geopolitical regions of Brazil: northeastern, southeastern and south. The Atlantic Rainforest province here adopted is divided in four sectors including the three previously recognized regions but with a somewhat different delimitation, each one with a defined centre of endemism, which better represents the floristic and physiognomic similarities of the natural regions, and slightly differentiating the geopolitical criteria (Figure 3.1). Three (Pernambuco, Bahia and Rio de Janeiro) of the 4 centres of endemism proposed agree with those recognized by Brown (1979), Mori et al. (1981) and Mori (1989). The fourth centre of endemism, in the southern sector, agreed with the hypothesis of Brown (1979) for the distribution of forest butterflies (Nymphalidae) and is based on the endemic taxa of Bromeliaceae and requires to be further supported with data from other families and genera.

The extent to which the Atlantic Rainforest in each sector penetrates to the interior is very variable and rather polemical, since this forest forms mosaics, enclaves and ecotones which interdigitate with formations and vegetation types from other domains such as the 'Cerrado' and 'Caatingas', seasonal forests, and gallery forests, and also because the level of disturbance and destruction. Indeed, Atlantic Rainforest appears to be a unsuitable name since it gives the idea of a uniform and continuous formation of typical tropical forest as defined by Richards (1952). A coordinated effort to better define in terms of physiognomy, structure and composition of the different types of forest and non-forest vegetation, incorporating phytogeographical criteria with regard to composition, phytosociology and phenology seems to be essential for future studies.

3.2. SOUTHEASTERN SECTOR

The southeastern sector of the Atlantic Rainforest province includes the State of Rio de Janeiro, and partially, the States of Espírito Santo, Minas

Gerais and São Paulo. This section can be delimited from Regencia, in the State of Espírito Santo, to Santos, in the State of São Paulo, with the interior boundaries extending from the margin of the river Doce to its source, near the locality of Antonio Dias, and following a line beteween Manhuaçu, Carangola, Muriaé, Santos Dumont, Varginha and Poços de Caldas in the State of Minas Gerais (Figure 3.2).

In this southeastern sector, the moist forest formation can be rather better defined due the well delimited topography (specially due to the influence of the highest coastal mountains), and in comparison with some other sectors, the forest formations in the southeastern sector can be better defined due to the uniform annual rainfall and temperature parameters (Figure 3.2; Tables 3.2.1, 3.2.2 and 3.2.3). Rio de Janeiro State is considered the most important centre of endemism (Smith, 1962; Gentry, 1979; Mori et al., 1981; Mori & Boom, 1981; Brown, 1976, 1977a, 1977b; Martinelli & Vaz 1988; Ab'Saber, 1989) with an extension of this centre to the mountains of the Espírito Santo State into the region enclosed by Santa Teresa, Domingos Martins and the eastern face of Caparaó mountain chain (personal observation).

In this southeastern sector the following formations occur: restingas, mangroves, granitic outcrops, moist forest, mesophytic forest and some enclaves of savannas and woodland formations from the Cerrado province. The types of vegetation of each formation of southeastern section of the Atlantic Rainforest province can be classified according the physical factors, altitudinal zonation, and floristic and physiognomic differences, although some of them intergrade as transitional zones. They are divided here as follows:

3.2.1. Restinga formation

This is interpreted here following the broad concept of Cain (1971) and the phytogeographical concept of Hueck (1972). Hueck recognized restinga as

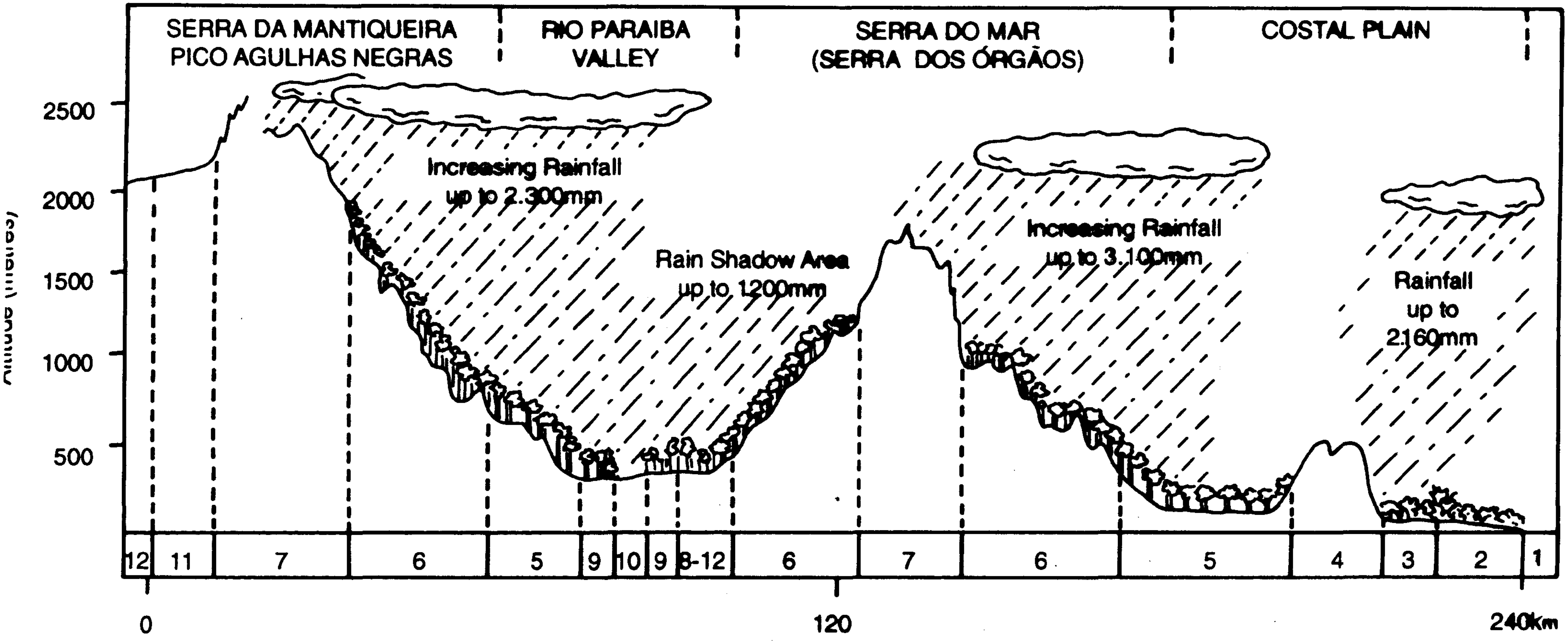

Figure 3.2. Diagramatic profile across the Atlantic Rainforest province in the Southern Sector (Rio de Janeiro to Minas Gerais boundary); 1) Atlantic Ocean; 2) 'restinga' formation; 3) mangrove; 4) coastal granitic outcrops; 5) lowland wet forest; 6) montane wet forest; 7) high montane grassland; 8-12) semideciduous forest with enclaves of 'cerrado'; 9) flooded lowland wet forest of Paraiba river margins; 10) Paraiba river; 11) Araucaria forest patches, and 12) mesophytic forests formation. Based in Hueck (1974); rainfall data from INM (1991).

Table 3.2.1. Climatic data of Atlantic Rainforest province, southeastern section, at Nova Friburgo, Rio de Janeiro State. (Study area 1, montane wet forest, 1000m).

MONTHS	TEMPERATURE (°C)					RELATIVE HUMIDITY (%)	RAINFALL (mm)	
	MEAN OF MAXIMUM	MEAN OF MINIMUM	MAXIMUM ABSOLUTE	MINIMUM ABSOLUTE	COMPENSATED MEAN		TOTAL (mm)	MAXIMUM (24 hours)
JAN	27.0	17.1	37.0	10.0	21.2	77	208.6	113.0
FEB	27.6	17.1.	33.3	7.0	21.4	78	167.2	149.6
MAR	26.9	16.8	35.8	9.1	20.9	78	151.0	96.6
APR	24.8	14.8	33.6	3.6	18.7	82	72.3	74.8
MAY	22.9	11.9	32.2	1.3	16.2	82	45.6	37.5
JUN	21.6	10.1	29.4	1.0	14.7	83	26.6	43.8
JUL	21.1	9.5	28.6	1.0	14.0	83	19.7	30.5
AUG	22.5	10.3	33.0	1.2	15.2	81	22.9	44.5
SEP	22.9	12.3	33.6	2.0	16.6	80	41.3	49.8
OCT	23.9	14.3	35.0	6.6	18.3	81	83.4	125.8
NOV	24.8	15.5	36.0	5.3	19.5	80	169.2	105.6
DEC	25.5	16.3	34.0	9.2	20.3	80	238.7	165.4
ANNUAL	24.3	13.8	37.0	1.0	18.1	80	1246.3	165.4

Source: National Metereologic Institute, Brazil (1961-1990).

Table 3.2.2. Climatic data of Atlantic Rainforest province, southeastern sector, at Petropolis, Rio de Janeiro State (Study area 3, montane wet forest, 800-1000m).

MONTHS	TEMPERATURE (°C)					RELATIVE HUMIDITY (%)	RAINFALL	
	MEAN OF MAXIMUM	MEAN OF MINIMUM	MAXIMUM ABSOLUTE	MINIMUM ABSOLUTE	COMPENSATE MEAN		TOTAL (mm)	MAXIMUM (24 hours)
JAN	27.5	17.7	33.8	11.0	n.a.	79	286.5	140.8
FEB	28.0	17.9	34.9	10.6	n.a.	77	200.1	140.0
MAR	26.7	17.1	32.6	10.8	n.a.	77	183.9	134.1
APR	24.2	14.9	30.6	6.4	n.a.	80	115.5	86.2
MAY	22.9	12.8	29.1	4.1	n.a.	83	55.2	55.0
JUN	21.9	11.2	28.2	1.4	n.a.	84	43.0	53.8
JUL	21.0	10.2	27.2	3.2	n.a.	85	47.2	61.9
AUG	22.7	11.7	30.8	4.7	n.a.	81	51.8	42.9
SEP	22.8	13.1	31.6	3.5	n.a.	80	81.1	60.5
OCT	23.7	14.8	33.8	6.8	n.a.	79	148.9	66.1
NOV	24.7	16.0	32.5	7.5	n.a.	77	219.4	134.0
DEC	25.9	17.2	33.6	10.2	n.a.	77	296.6	107.3
ANNUAL	24.3	14.6	34.9	1.4	-	80	1729.4	140.8

Source: Metereological National Institute, Brazil (1865-1987).
n.a. - not available

Table 3.2.3. Climatic data of the Atlantic Rainforest province, southeastern sector, at Paraty, Rio de Janeiro State (Study area 1, lowland wet forest, restinga, mangrove and granitic outcrops, sea level).

MONTHS	TEMPERATURE (°C)					RELATIVE HUMIDITY (%)	RAINFALL	
	MEAN OF MAXIMUM	MEAN OF MINIMUM	MAXIMUM ABSOLUTE	MINIMUM ABSOLUTE	COMPENSATE MEAN		TOTAL (mm)	MAXIMUM (24 hours)
JAN	29.8	22.6	38.5	15.3	26.9	81	276.4	285.6
FEB	30.4	23.1	39.3	17.1	26.4	80	240.2	203.8
MAR	29.5	22.5	37.4	16.3	25.8	81	237.1	164.5
APR	27.6	20.8	35.3	12.8	24.0	82	189.5	191.2
MAY	26.2	18.9	35.1	12.8	22.2	82	109.0	105.0
JUN	25.0	17.1	32.8	9.8	20.6	82	78.3	76.1
JUL	24.6	16.5	33.8	10.1	20.2	81	76.2	141.0
AUG	25.0	17.2	36.0	9.4	20.7	81	78.2	138.9
SEP	24.9	18.2	36.4	11.0	21.3	82	116.0	73.4
OCT	25.6	19.3	35.8	13.4	22.3	83	141.1	89.0
NOV	27.0	20.4	37.2	13.7	23.5	82	166.6	103.2
DEC	28.6	21.7	38.8	14.4	24.9	82	265.0	191.4
ANNUAL	27.0	19.8	39.3	9.4	23.2	82	1976.7	285.6

Source: Metereological National Institute, Brasil (1961-1990).

Table 3.2.3. Climatic data of the Atlantic Rainforest province, southeastern sector, at Paraty, Rio de Janeiro State (Study area 1, lowland wet forest, restinga, mangrove and granitic outcrops, sea level).

MONTHS	TEMPERATURE (°C)					RELATIVE HUMIDITY (%)	RAINFALL	
	MEAN OF MAXIMUM	MEAN OF MINIMUM	MAXIMUM ABSOLUTE	MINIMUM ABSOLUTE	COMPENSATE MEAN		TOTAL (mm)	MAXIMUM (24 hours)
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JUL	24.6	16.5	33.8	10.1	20.2	81	76.2	141.0
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SEP	24.9	18.2	36.4	11.0	21.3	82	116.0	73.4
OCT	25.6	19.3	35.8	13.4	22.3	83	141.1	89.0
NOV	27.0	20.4	37.2	13.7	23.5	82	166.6	103.2
DEC	28.6	21.7	38.8	14.4	24.9	82	265.0	191.4
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Source: Metereological National Institute, Brasil (1961-1990).

Table 3.2.3. Climatic data of the Atlantic Rainforest province, southeastern sector, at Paraty, Rio de Janeiro State (Study area 1, lowland wet forest, restinga, mangrove and granitic outcrops, sea level).

MONTHS	TEMPERATURE (°C)					RELATIVE HUMIDITY (%)	RAINFALL	
	MEAN OF MAXIMUM	MEAN OF MINIMUM	MAXIMUM ABSOLUTE	MINIMUM ABSOLUTE	COMPENSATE MEAN		TOTAL (mm)	MAXIMUM (24 hours)
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MAY	26.2	18.9	35.1	12.8	22.2	82	109.0	105.0
JUN	25.0	17.1	32.8	9.8	20.6	82	78.3	76.1
JUL	24.6	16.5	33.8	10.1	20.2	81	76.2	141.0
AUG	25.0	17.2	36.0	9.4	20.7	81	78.2	138.9
SEP	24.9	18.2	36.4	11.0	21.3	82	116.0	73.4
OCT	25.6	19.3	35.8	13.4	22.3	83	141.1	89.0
NOV	27.0	20.4	37.2	13.7	23.5	82	166.6	103.2
DEC	28.6	21.7	38.8	14.4	24.9	82	265.0	191.4
ANNUAL	27.0	19.8	39.3	9.4	23.2	82	1976.7	285.6

Source: Metereological National Institute, Brasil (1961-1990).

a formation with a myriad of types and subtypes of vegetation and plant communities occurring on sandy sediments of marine or aeolian origin, that are found along the Brazilian coast. As pointed out by Araujo (1992) the major difficulties in determining a classification system of vegetation types and communities for all sandy coastal plain vegetation in tropical Brazil are (1) lack of floristic, physiognomic and ecological data for much of the coast and (2) lack of consensus as to what constitutes a restinga formation, which may include beach ridges, barrier beaches, bars, spits, dunes and swales.

The restinga formation of the southeastern sector include a diverse array of vegetation found on sandy soils on the narrow coastal plain. Sometimes such restinga extends considerably to the interior, as in the Cabo Frio region in the State of Rio de Janeiro, where it occurs between high tide level and the lowland wet forest on lateritic soil further inland. It sometimes interdigitates with mangroves, lowland wet forest, and granitic outcrops. The concept adopted here includes beaches, dunes, open shrubs or thicket vegetation and a low forest vegetation with two sub-types of vegetation. The most important are:

a) Herbaceous beach and dune vegetation type, dominated by *Alternanthera maritima*, *Hydrocotyle bonariensis*, *Ipomea pes-caprae*, *Ramirea maritima*, *Blutaparon portulacoides*, *Mariscus pedunculatus* and *Sporobulus virginicus*. (Hueck, 1972; Araujo & Henriques, 1984).

b) Shrubby open restinga just inland from the beach zone, which can be found in continuous extensions or in small patches, forming islands of thicket vegetation with *Allagoptera arenaria*, *Sophora tomentosa*, *Byrsonima sericea*, *Chrysobalanus icaco*, *Protium brasiliensis*, *Opuntia* spp., *Gaylussacia brasiliensis*, *Eugenia* spp., *Myrcia* spp. as the most common taxa (Araujo & Henriques, 1984 and personal observation). Bromeliads encountered in this area are *Neoregelia cruenta*, *N. compacta*, *Aechmea nudicaulis* var. *nudicaulis* and *Vriesea neoglutinosa*.

c) Shrubby closed restinga, comprising a more diversified taller zone of shrubs and small trees with Sideroxylum obtusifolium, Schinus terebentifolius, Ouratea cuspidata, Ormosia nitida, Andira frondosa, Machaerium spp., Protium spp., Rheedia brasiliensis, Clusia fluminensis, Aechmea distichantha var. distichantha, and Bromelia anthiacantha (Hueck, 1972; Araujo & Henriques, 1984; personal observation). Hueck (1972) and Ule (1901) distinguished two different sub-communities in this type: restinga with dominance of Clusia and restinga with dominance of Myrtaceous species. Both authors agreed that the restinga of Clusia is a more advanced stage of development, forming a transitional zone to the restinga forest.

d) Restinga forest is a low forest composed of a combination of tree species from the proceeding zones and adjacent lowland wet forest. Communities of Arecastrum romanzoffianum are frequent together with Pseudopiptadenia contorta, Pterocarpus rohrii, Guettarda virbunoides, Alseis involuta, Erythroxylum pulchrum, E.ovalifolium, Guapira opposita, Maytenus obtusifolia, Myrrhinium atropurpureum, Cupania emarginata, Myrcia lundiana, Clusia hilaireana, Aechmea sphaerocephala, Vriesea procera var. procera, Vriesea sucrei, Cryptanthus sinuosus, C.acaulis var. acaulis among others species are the most common (Araujo, 1992).

Along the coastline to the south of the city of Rio de Janeiro, only a narrow band of restinga can be found in some areas, because coastal mountains rise abruptly, covered by lowland wet forest or with maritime outcrops.

Restinga formation has been studied by many authors and species lists have been prepared for various areas and types of vegetation along the eastern coast of Brazil and especially in the southeastern section as Araujo & Henriques (1984), Hueck (1955), Pereira (1990), Ule (1901), Araujo & Peixoto (1977), and Esteves (1980).

3.2.2. Coastal Granitic outcrops

In the southeastern and southerly sector, the Brazilian coastline is punctuated by a series of massive granitic outcrops which either interrupt the restinga and lowland wet forests, or form small islets close offshore. The vegetation of such granitic outcrops in some areas of Rio de Janeiro State has been described by Carauta & Oliveira (1985) who emphasized the dominance of species of the families Cyperaceae, Gramineae, Bromeliaceae, Cactaceae, Orchidaceae, Velloziaceae and Compositae. The coastal granitic outcrops thus show some floristic similarities with the high montane outcrops (high montane grassland), but can be clearly differentiated by the altitudinal level, the xerophytic character of the granitic outcrop due its proximity to the sea and, by the floristic composition at the species level, despite of some similarities in terms of physiognomy and composition at the family level.

Fontoura et al. (1991) showed that 8.3% of 314 Bromeliaceae taxa which occur in the Rio de Janeiro State, are found on granitic outcrops, with 1.9% of these being endemics. In the whole southeastern sector there are 3% (12 taxa) of 444 taxa that occur in this sector, with 33% endemic for the granitic outcrops.

3.2.3. Mangrove formation

Mangrove vegetation in the southeastern sector occurs as dense tree communities, or more rarely as shrubby communities, in areas where the substrate is saline, flat, and muddy. These conditions are often met behind sand bars and at the mouths of coastal rivers. Similarly, in all inlets, small and large bays, such as Guanabara and Ilha Grande bay in Rio de Janeiro State, mangrove vegetation can be found. As with the restingas, in zones where the mountain scarp is very near the sea, the mangrove is limited to narrow areas.

In southeastern sector, mangroves are formed predominantly by *Laguncularia racemosa*, *Avicenia tomentosa*, *Hibiscus tiliaceus*, and the fern *Achrostichum aureum*. Bromeliaceae species also occur as epiphytes in mangroves, such as *Quesnelia marmorata*, *Vriesea gigantea*, *Tillandsia gardneri*, *T. stricta* var. *stricta*, among others.

The original distribution of mangrove in the southeastern sector has, like the restinga, been greatly reduced by anthropomorphic influence, particularly since its tree species provides excellent fuel wood. The mangroves of eastern Brazil have been studied by Luederwoldt (1919), Stellfeld (1945), Bigarella (1946), Vasconcelos (1949), Lamberti (1969), and Andrade-Lima (1970) among others.

3.2.4. Moist forest formation

The moist forest formation in the southeastern sector, in its primitive form, usually occurred behind the line of restinga and mangroves but in some areas extended to the beach, and covered the foothills and slopes of the mountains to around 2,000 m of altitude. To the interior, the moist forest formation interdigitated with a mesophytic forest formation, sometimes forming a complex transitional zone, or interpenetrating between other types of formations and, in some cases, abruptly, with a non defined ecotone zone.

The following vegetation types are been included in the moist forest formation in the southeastern sector:

a) Lowland wet forest, which extends on the coastal plain and foothills of the mountain ranges, from sea level to 600m of altitude. In its primitive form it is characterized by trees of 35-40 m, with a high diversity of species, and a richness of lianas and epiphytes. In general, this forest is well represented by species of Leguminosae, Bignoniaceae, Rubiaceae, Sapotaceae, Lauraceae, Myrtaceae, Meliaceae and Palmae as tree families and, Orchidaceae, Bromeliaceae, Gesneriaceae, Piperaceae and Cactaceae as epiphytic families. The Leguminosae presents the highest number of species, with genera such as Newtonia, Parapiptadenia, Hymenaea, Melanoxylum, Myrocarpus, Dalbergia, Machaerium, Centrolobium, Cassia, Swartzia, Inga, among others.

3.2.4.1. Lowland wet forest

In the southeastern sector of the Atlantic rainforest domain, the lowland wet forest can be subdivided in two different types: (1) the lowland wet forest on well drained soils, with a deep layer of litter, specially on the foothills of the mountains or small elevations on the coastal plain, and (2) periodically flooded lowland forest, which has a markedly different flora, often dominated by Calophyllum brasiliensis, Symphonia globulifera and Tabebuia cassinoides.

Recently, the Botanic Garden of Rio de Janeiro, through the development of the Atlantic Rainforest Program (PMA, 1992) has produced floristic and phytosociological inventories in the forest vegetation types of the moist forest formation in the southeastern sector. The sample areas were surveyed by means of quadrats of one hectare, established along the altitudinal gradient. In the lowland wet forest the studies where carried out in the Ecological Station of Paraiso, Magé County, Rio de Janeiro State, between 60-500 m altitude and this survey has indicated the uniqueness of many species and the high diversity for this forest type.

The percentage of endemic species in this lowland wet forest on well-drained soils was relatively low (35.4%) in comparison with the montane wet forest of the Macaé de Cima Ecological Reserve (58.5%), inventoried by the Atlantic Rainforest Program. In the lowland wet forest at the Ecological Station of Paraiso 491 vascular taxa were observed with the dicots representing 81% of the total sampled (Table 3.2.4). The Rubiaceae was the most diverse family with 14 genera, followed by Leguminosae, Lauraceae and Myrtaceae (Table 3.2.5). The distribution pattern of the species of Paraiso Ecological Station is shown in the Table 3.2.6.

Within the one hectare sampled at Paraiso Ecological Station, there was a total of 1606 individuals distributed in 47 families, 103 genera and 179 species. The families Myrtaceae (225 individuals), Palmae (177), Euphorbiaceae (126), Rutaceae (109), Sapotaceae (94) and Rubiaceae (88) represented 55,3% of the individuals sampled. The families with the greater number of species were Lauraceae (20 species), Myrtaceae (18), and Leguminosae (15). The other families which contributed significantly in the floristic composition were Meliaceae, Moraceae, Violaceae and Myristicaceae (PMA, 1992).

Table 3.2.4. Number of species of Paraiso Ecological Station, Magé, Rio de Janeiro State.

GROUPS	No. FAMILIES	SPECIES (%)
Pteridophytes	15	50 (10)
Monocotyledons	06	45 (09)
Dicotyledons	67	396 (81)
TOTAL	88	491

Source: Floristic and Phytosociological Project/Atlantic Rainforest Program Report (1992).

Species with high frequency and density values were Euterpe edulis, Chrysophyllum flexuosum, Neoraputia magnifica var. magnifica, Senefeldera multiflora, Eugenia microcarpa and Eugenia subavenia, making together 26.7% of total density. Euterpe edulis alone represented 10.1% (PMA, 1992). Amongst the emergent trees encountered, Hymenaea courbaril (36 m), Chrysophyllum lucentifolium (35 m), Ficus gameleira (35 m), Myrocarpus frondosus (32 m) and Pseudopiptadenia inaequalis (32 m) were notable (PMA, 1992).

The diversity index calculated was H'=4,4 (Shannon-Weaver index: Shepherd, 1988), which was higher than to the montane wet forest and reflects the greater number of species with fewer individuals (PMA, 1992).

Table 3.2.5. Main families of vascular species of the Paraiso Ecological Station, Magé, Rio de Janeiro.

FAMILIES	No. OF GENERA	No. OF SPECIES
Rubiaceae	14	50
Leguminosae	30	48
Lauraceae	05	31
Myrtaceae	09	31
Dryopteridaceae	11	19
Moraceae	08	17
Araceae	06	15
Euphorbiaceae	09	15
Sapotaceae	06	15
Piperaceae	03	14
Meliaceae	04	11
Orchidaceae	07	10
Bromeliaceae	06	10
Diverse	118	220
Total	239	491

Source: Floristic and Phytosociological Project/Atlantic Rainforest Program (1992).

Table 3.2.6. Distribution pattern of the species of Paraiso Ecological Station, Magé, Rio de Janeiro State.

DISTRIBUTION	No. OF SPECIES (%)
Endemics of Paraiso Ecological Station	01 (0.2%)
Endemic of moist forest formation of Rio de Janeiro State	57 (11%)
Endemic of Atlantic Rainforest Province	174 (35.4%)
Large distribution	317 (64.6%)

Source: Floristic and Phytosociological Project/Atlantic Rainforest Program (1992).

The lowland wet forests of the southeastern section of the Atlantic Rainforest province have been inventoried floristically and phytosociologically by Soares & Ascoly (1979), Pagano & Leitão Filho (1987), Guedes (1989), among others.

3.2.4.2. Montane wet forest

This type of moist forest formation occupies the major part of the southeastern sector. The lowest altitudinal limit is around 600 m and the upper limit varies according to the mountain range, from 1,700 m in the Serra do Mar, on the boundary of Rio de Janeiro and São Paulo States, 1,800 m in Serra dos Órgãos, and up to 2,000 m in the Itatiaia Massif of the Serra da Mantiqueira (Segadas-Vianna & Dau, 1965; Hueck, 1972; Martinelli, 1989).

The montane wet forest in the southeastern sector is characterized by the occurrence of cloud-mist and a high rainfall, between 2,000 - 2,500 mm (Fig. 3.3), virtually distributed throughout the year, but with a relatively defined dry season during the months of June and July.

The montane wet forest can be divided in two subtypes: (1) The popularly called "mata de encosta" (slopes forest) which occurs on the slopes of the mountains as illustrated in the Figure 3.2, and (2) the so-called "mata de neblina" (mist forest), which occurs in the upper altitudinal limits on the ridges of the highest mountains and around the high montane grassland. Details of the physiognomy, floristic composition and structure of both types still need to be studied. The "mist forest" is characterized by tall trees, mainly represented by Weimannia organensis (Cunnoniaceae), Drimys winterii (Winteraceae), Roupala spp. (Proteaceae), and by the richness of epiphytic species of the families Bromeliaceae, Orchidaceae, and Gesneriaceae. The limits between the "slopes forest" and the "mist forest" are variable but it usually coincides with the upper limit of altitudinal distribution of Euterpe edulis, which is found from the lowland wet forest to the upper limits of "slopes forest", as observed by Hueck (1972).

Some changes in physiognomy and floristic composition occur, in the montane wet forests on the west facing slopes due to lower rainfall in this area, together with a relatively well-defined three months of semi-dry period (Hueck, 1972; personal observation).

A series of floristic and phytosociological inventories were made in 1990 in the montane wet forest on the E slopes of Serra dos Órgãos, at 1,000 - 1,100 m of altitude, in the Macaé de Cima Ecological Reserve, Rio de Janeiro State by the Atlantic Rainforest Program of the Rio de Janeiro Botanic Garden. Preliminary results from this survey emphasise de importance of this vegetation, as well as the high level of endemism. The inventory was concentrated in two quadrats of one hectare each, one representing a well preserved forest (primary forest) and the other in a selectively exploited forest, which had some of the biggest trees removed 40 years ago (secondary forest).

The primary forest inventory found that the bryophytes are represented by 28 families, 39 genera and 55 species (6.4% of the known local flora); the pteridophytes by 17 families, 36 genera and 76 species (8.9%) and the phanerogams by 103 families, 94 genera and 727 species (84.7%).

A preliminary survey of the vascular epiphytic community, identified 144 species (40 pteridophytes, 64 monocots and 40 dicots). Among these epiphytes, 42% are endemic to the moist forest formation of the Rio de Janeiro State. The families of vascular epiphytes were mainly Orchidaceae, Bromeliaceae and Polypodiaceae (Table 3.2.7).

The distribution patterns of the 678 species identified to specific level indicate a significant number of endemic species for the montane wet forest (26% of pteridophytes and 63% of phanerogams); 126 species were narrow endemics, restricted to the moist forest formation in the Rio de Janeiro State, and 19 of these species are only known from the Macaé de Cima Ecological Reserve.

To date, 13 new species have been discovered some of them not yet described, as well as 121 rare and endangered species and 229 species of economic or medicinal value.

A total of 2,532 individuals of phanerogams were sampled in the phytosociological inventory of the well-preserved montane wet forest (Quadrat I) and the analysis of the species richness showed the following families to be representative of the area: Myrtaceae, Lauraceae, Melastomataceae, Rubiaceae, Leguminosae, Monimiaceae and Solanaceae. A high diversity index (Shannon-Weaver index: Sheperd, 1988) was also obtained for this area (H' = 3,99), as well as a significant number of dead individuals (147).

In the sample area of disturbed forest (Quadrat II), 2,347 individuals of phanerogams were encoutered and the analysis of species richness showed Lauraceae, Melastomataceae, Rubiaceae, Leguminosae, Compositae and Flacourtiaceae as the most important families. The diversity index (H') in this area was 3,76 and the number of dead individuals was significantly less (11). These surveys at Macaé de Cima Ecological Reserve demonstrated the richness of tree species of montane wet forest whem compared with other tropical rainforest inventories (Table 3.2.8).

The montane wet forest, in both of its subtypes, is characterized by the greatest diversity for the Bromeliaceae, in the southeastern sector, as shown in the Appendix 1.

Climbing phanerogams also presented high species diversity. A comparison of the vines which occur in the two study sites (Quadrat I and II) showed marked differences between floristic composition and dispersal mechanisms. This demonstrates the profound changes caused by man, even in the areas which are in an advanced stage of regeneration.

The large number of species which are rare, endangered or of economic importance demonstrates the significance of the remnant Atlantic montane wet forest, found in Macae de Cima. Many economically important species have had their populations significantly reduced by over-exploitation. The threat of extinction of these species is great and prevention measures require the increase of germoplasm conservation and conservation-oriented educational programmes for local inhabitants.

Table 3.2.7. Families of vascular epiphytes of Macaé de Cima Ecological Reserve, Rio de Janeiro State.

FAMILIES	No. OF GENERA	No. OF SPECIES
Orchidaceae	09	34
Bromeliaceae	07	21
Polypodiaceae	06	16
Araceae	02	07
Cactaceae	03	07
Gesneriaceae	02	05
Hymenophyllaceae	02	05
Aspleniaceae	01	04
Dryopteridaceae	01	04
Lycopodiaceae	01	04
Piperaceae	01	04
Begoniaceae	01	02
Cornaceae	01	01
Euphorbiaceae	01	01
Melastomataceae	01	01
Ophioglossaceae	01	01
Rubiaceae	01	01
Vittariaceae	01	01
TOTAL	52	119

Source: Floristic and Phytosociological Project/Atlantic Rainforest Program (1990).

Table 3.2.8. Comparison of tree species richness of Macaé de Cima Ecological Reserve with other tropical rainforest inventories.

MACAE DE CIMA	CAPEIRA	ST. ROSA	JAUNECHE	BARRO COLORADO	RIO PALENQUE
368 (51%)	97 (21%)	206 (31%)	166 (32%)	425 (32%)	253 (30%)

Source: Floristic and Phytosociological Project/Atlantic Rainforest Program (1990).

3.2.5. High montane grassland

Hueck (1972) was the first author to recognize the high montane grassland as a type of vegetation of the Atlantic moist forest formation, and recently by Martinelli (1989) and Martinelli et al. (unpublished data) who undertook floristic and phytogeographic studies in these areas. This vegetation type is situated on the top of the mountain ranges of southeastern section of the Atlantic rainforest domain, and is characterized physiognomically as a grassland ('alpine meadow'), occurring on the highest mountains between 1,500 m to 2,800 m, varying according to the chain of mountains. During the winter and dry season, the temperature of these areas drops dramatically, with occasional frosts, with the opposite in the summer and rainy season when the temperature increases during the day, and a thick cloud forms during the night. In these areas the vegetation can be found growing on a rocky substrate, forming "islands" of vegetation, frequently in very steep rock cliffs, and with little or no soil formation, or in shallow soils of small plateaus, with a few deeper soils, according with the topography of the mountain, which may be in the form of domes, accidented peaks or upland plateaus, each one with different plant communities. The adjacent montane wet forest forms a buffering zone around the high montane grassland. In general, the crystaline rocks are formed by gneisse-granite, encrusted with quartzite. The shallow soils of the plateaus have a high aluminium content mixed with clays and sandy gravel.

This type of vegetation is distributed on the coastal mountain range. To the interior, they gradually change in floristic composition, with a mixed flora from the high montane grassland and with elements of the rocky open savannas named "campos rupestres" of the Cerrado province, as in the mountain chains of the interior boundary of southeastern sector (Serra do Caparaó, Serra do Ibitipoca and Serra da Mantiqueira).

The flora of the high montane grassland of the southeastern sector is formed by herbaceous and shrubby species of Gramineae, Compositae, Orchidaceae, Bromeliaceae, Melastomataceae, Cyperaceae and Velloziaceae as the most important families. The number of endemic species is very high (Martinelli & Vaz, 1988; Martinelli, 1989). The study carried out in six different areas of high montane grassland by Martinelli (1989) and Martinelli et al. (unpublished data) showed that some of the endemic species are characterized as paleoendemics: Worsleya rayneri (Amaryllidaceae), Glaziophyton mirabile (Gramineae), Prepusa conata (Gentianaceae), Gaultheria organensis (Ericaceae) among others, which are confined to a single mountain top or in a short stretch of mountain terrain. These six areas a total of 1603 species was identified, with 6.12% of them as narrow endemics (exclusive to a single mountain, sensu Cain, 1951), and 18.5% as endemic to this type of vegetation (Table 3.2.9).

Fontoura et al. (1991) observed that 13.7% of the 314 Bromeliaceae taxa occurring in the Rio de Janeiro State are found in the high montane grassland, of which 4.1% are endemics to this type of vegetation. In our own surveys, we found that of the 444 taxa for the southeastern sector, 13% are endemic to this type of vegetation.

Table 3.2.9. Floristic data for six areas of high montane grassland of southeastern sector of Atlantic Rainforest province.

AREAS	TOTAL SPECIES	NARROW ENDEMICS	ENDEMIC OF VEGETATION TYPE	ENDEMIC OF ATLANTIC RAINFOREST PROVINCE
Cuca	227	6 (2%)	27 (12%)	72 (32%)
Frade de Macaé	124	5 (4%)	22 (18%)	49 (40%)
Desengano	275	24 (9%)	62 (22%)	57 (21%)
Campo das Antas	347	13 (4%)	66 (19%)	127 (37%)
Bocaina	215	6 (3%)	30 (14%)	74 (30%)
Itatiaia	415	44 (11%)	88 (21%)	126 (30%)
TOTAL	1.603	98 (6.1)	295 (18.4%)	505 (31.5%)

Source: Redraw from Martinelli (1989).

3.2.6. Mesophytic forest formation

The mesophytic forest formation of the southeastern sector presents the same problems and difficulties that are found in the other sectors. It has been almost completely destroyed by coffee and sugar-cane plantations in the past, and more recently by cattle raising along the interior boundary of this section. Timber and firewood extraction, and charcoal production, have also contributed to the destruction of this forest.

The mesophytic semideciduous forest occurred in the past in the Paraiba River valley, in the State of Rio de Janeiro, together with small enclaves of Cerrado vegetation, and merged with the gallery forests to the interior, which extend into the Cerrados of central Brazil. The concept here adopted is to include in the Atlantic Rainforest domain the transitional zone between the Serra do Mar and the Cerrado province. The few floristic data disponable indicate a relative dominance of species of moist forest formation occurring in the deciduous and semideciduous forest types as showed in the list of species of Negreiros et al. (1974), Gibbs & Leitão Filho (1978), Martins (1979), Gibbs et al. (1980), Matthes (1980), Assumpção et al. (1982), to the mesophytic forest areas of São Paulo State. A definitive limit for the interior boundary of the southeastern section where the mesophytic forest formation occurs still requires further study to provide a precise limit.

In the southeastern sector, the mesophytic forest formation presents 16 taxa of Bromeliaceae (4%) of a total of 444 taxa for this section, with 7 (44%) endemic for this formation. (Appendix 1). A preliminary analysis of distribution and endemism of Bromeliaceae of the southeastern Atlantic Rainforest shows that this sector is the most important region for the Bromeliaceae, with a very well defined centre of endemism placed in the moist forest formation of the Rio de Janeiro State and the mountainous areas of Espírito Santo State.

Of a total of 789 taxa of Bromeliaceae which occur in the Atlantic Rainforest province, 444 (56%) were found in the southeastern section, with 325 taxa (73%) endemics for this section. The Rio de Janeiro State presents the highest number of species: 277 (62%) of the total number for this sector, with the biggest concentration of endemic taxa (Appendix 1). The endemic species of the southeastern sector are distributed mainly in the moist forest formation, with 340 (76%) of 444 taxa, followed by restinga: 52 (12%), high montane grassland: 24 (5%), mesophytic forest 16 (4%) and granitic outcrops: 12 (3%).

3.3. NORTHEASTERN SECTOR

The northeastern sector of the Atlantic rainforest province includes the States of Rio Grande do Norte, Paraiba, Pernambuco, Alagoas, Sergipe and N of Bahia. This section is delimited from Cape São Roque in Rio Grande do Norte to Salvador, north of Bahia State, and extending to the interior for some 30 - 80 Km from the coast, where the Atlantic rainforest forms an ecotone with the Caatinga domain. Inland extensions may be more extensive along the margins of the principal rivers in the southern part of this area.

This NE sector includes small remnants of once more extensive moist forest formations, represented by lowland wet forest between sea level and 200m and the montane wet forest called 'brejo forest', between 200 - 800 m. As usual, the coastal dunes with shrubby restinga and woodland restinga forest types occurs on coastal sands, with mangrove formation in areas with estuarine mud flats. The 'brejo forest' is found on the edge of plateaus in the States of Paraiba and Pernambuco, forming enclaves within the Caatinga domain (Figure 3.3). Andrade-Lima (1953, 1954, 1970), Braga (1960), Kuhlmann (1977), Mori & Silva (1979), Mori & Boom (1981), RADAMBRASIL (1981), and Mayo & Fevereiro (1982) among others, have contributed to the floristic and phytogeographic knowledgement of this sector.

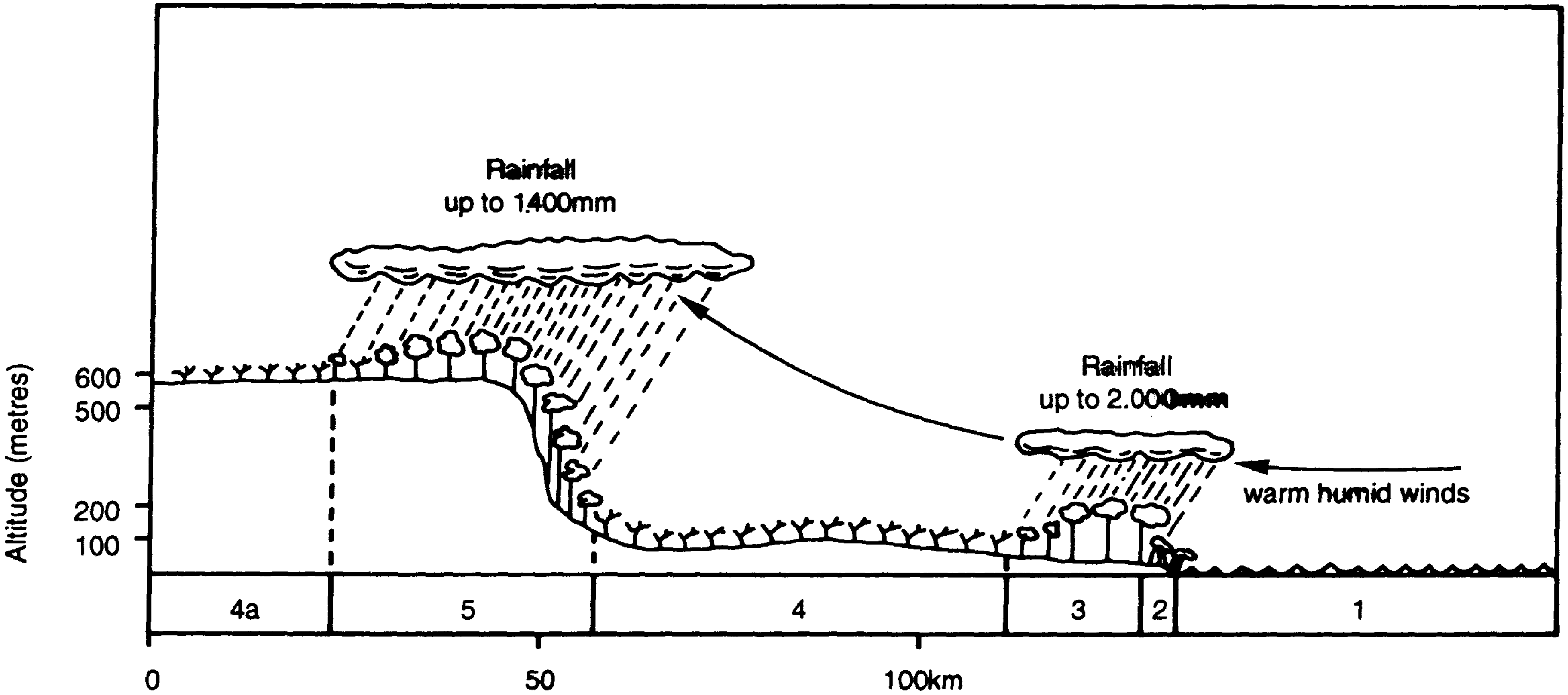


Figure 3.3. Diagramatic profile across the Atlantic Rainforest province in the Northeastern Sector (Paraiba State): 1) Atlantic Ocean; 2) Mangrove; 3) lowland wet forest; 4) enclave of 'caatinga; 5) montane wet forest ('brejo' forest); 4a) Caatinga province. Source: Mayo & Fevereiro (1982), modified.

The northeastern sector presents a centre of endemism located in the lowland wet forest, montane wet ('brejo') forest , and in the restinga formation in the State of Pernambuco and part of Paraiba. This endemic centre also contains a relatively high number of disjunct species with the Amazonian rainforest domain (Prance, 1979; Gentry, 1979; Mori, 1989). An analysis of bromeliad distributions (Appendix 1) indicates that Pernambuco moist forest formation is only a small centre of endemism for the Bromeliaceae, with 78 taxa (10%) of a total of 789 of the Atlantic rainforest province, of which, 28 are endemic (36%) and 40 taxa occur on the moist forests formation (63%), 20 on the restinga, and 9 taxa (11%) on mesophytic forests formation.

3.4. EASTERN SECTOR

The Atlantic rainforest domain in the eastern sector occurs in part of the states of Bahia, Minas Gerais and Espírito Santo, with the limits from south of Salvador to the outskirts of Fundão, north of Espírito Santo, along the coast, and extending to the interior to the edge of the Espinhaço mountain chain, forming an irregular line near Jequié and Itambé, in the State of Bahia, and Bandeira, Águas Formosas, Teófilo Otoni and Governador Valadares, in the State of Minas Gerais, then in direction to Colatina on the margins of Rio Doce to the locality of Regencia, on the coast. This sector also presents the moist forest and mesophytic forest formations but montane wet forest is lacking due to the absence of barrier mountain chain, as indicated to the north part of this sector in Figure 3.4. The lowland wet forest is the most important vegetation of this sector, present today just in a form of fragments, included in national parks, biological reserves and other conservation units.

Such lowland wet forest occurs on Tertiary sediments of the Barreiras formation, and is known locally as 'Mata de Tabuleiro' ('Tabuleiro' forest). Some Amazonian moist forest also occurs on such Tertiary sediments, and

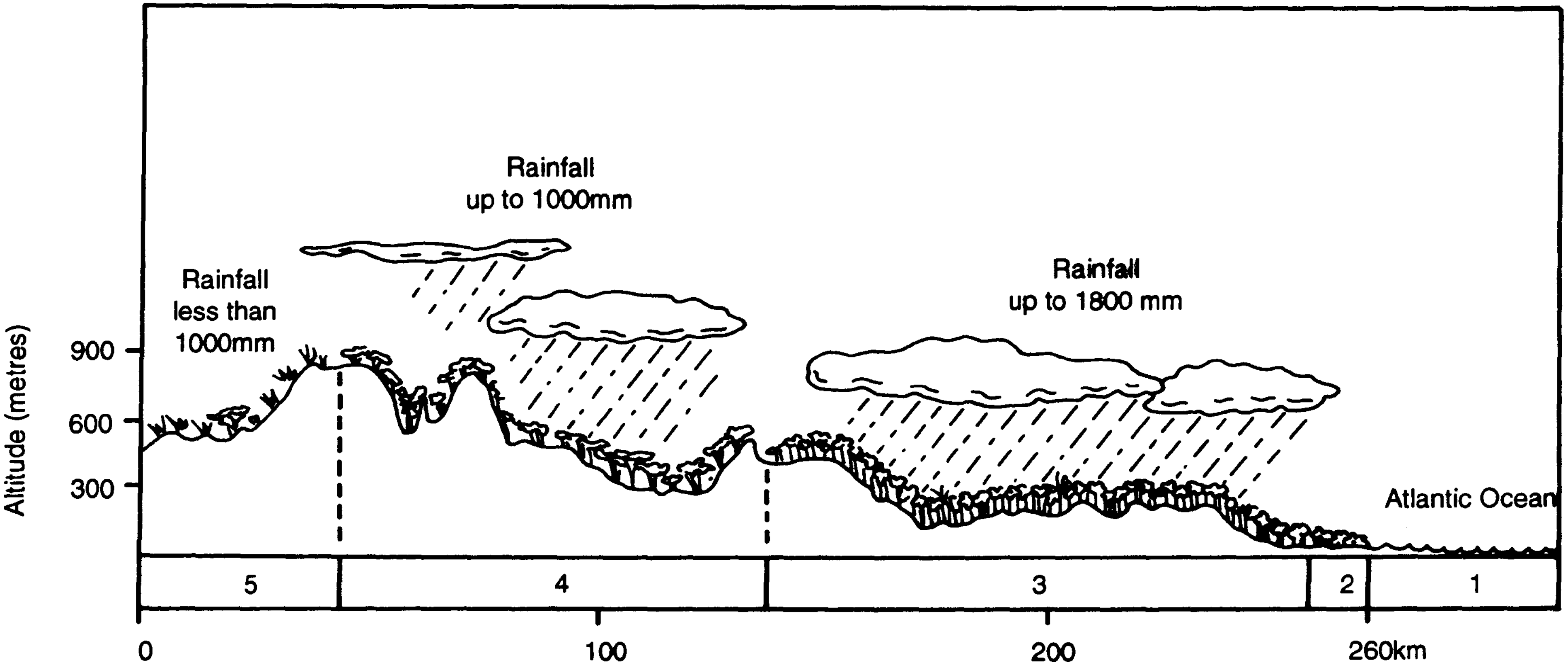


Figure 3.4. Diagramatic profile across the Atlantic Rainforest province in the Eastern Sector (Ilheus to Vitoria da Conquista): 1) Atlantic Ocean; 2) 'restinga'and mangrove; 3) lowland wet forest; 4) mesophytic forests formation, and 5) Caatinga province. Source: Mori (1989), modified.

there are some striking structural and floristic similarities between "terra firme" forest of the Amazonian rainforest domain and the 'Tabuleiro' forest of S Bahia and N of Espírito Santo. However, it would seem that the 'Tabuleiro' forest also contains elements from inland semideciduous forest and other vegetation types. It also merges with a mesophytic forest formation located in the foothills of the Espinhaço mountain chain, where it interdigitates with Caatinga and Cerrado vegetation. Authors who have contributed to the knowledgement of the floristic and the vegetation of this sector as Gouvea et al. (1976), Vinha et al. (1976), Mori & Boom (1981), Mori et al. (1981), Mori (1989), Carvalho (1981), among others.

The centre of endemism for this E sector occurs in area where the 'Tabuleiro' forest intermingles with small extensions of restinga forests, in the coastal plain from Linhares, N of Espírito Santo to Ilhéus, S of Bahia (see Figure 3.1). The Bromeliaceae is well represented with 112 taxa representing 14% of the 789 taxa to the Atlantic Rainforest province, of which 68 (61%) are endemic, distributed between moist forest formation: 74 (66%), restinga: 29 taxa (26%), and mesophytic forest formation: 9 taxa (8%) (Appendix 1). This centre of endemism for Bromeliaceae agrees with the centre of endemism for other families suggested by Brown (1979), Calderon & Soderstrom (1980), Mori et al. (1981) and Mori (1989).

3.5. SOUTHERN SECTOR

This sector includes part of the State of São Paulo, which is located in the southeastern geopolitical region, and also the States of Paraná, Santa Catarina and Rio Grande do Sul. The limits can be established from Santos, in the State of São Paulo, to the south of Rio Grande do Sul, and penetrating to a variable and imprecise distance into the hinterland, perhaps extending to the

Missiones region of Argentina and southern Paraguay, on the basin of Uruguay and Paraná rivers, and also penetrating to more inland areas in gallery forests.

The vegetation types included in this sector are very complex, and include different types of lacustrine vegetation on the coastal plain of Rio Grande do Sul (named 'banhados'), in addition to moist forest formation, restinga formation, mangrove formation and mesophytic semideciduous forest formation to the interior, as in the previous sectors (Figure 3.5).

The vegetation types present in the moist forest formation are: lowland wet forest, montane wet forest (slope forests and mist forest), Araucaria forest and Podocarpus forest, and high montane grassland. The restinga and mangrove formations present the same types of vegetation that occur in the other sectors. Some not very well defined mesophytic, and semideciduous forest types occur on the boundaries of Paraná, Santa Catarina, Rio Grande do Sul and north of São Paulo State. The gradual changes in the floristic composition and the lack of precise floristic and phytosociological inventories of the vegetation types in this zone of vegetational contact, do not permit a definite limit to the interior boundary of the Atlantic Rainforest in this sector.

The present complex sitution with regard to the limits of the Atlantic Rainforest province, has its origins in part due to the climatic fluctuations of the late Quaternary period (Bigarella, 1974), during which time contractions and expansion of humid forest areas occurred, but it is also compounded by the influence of agriculture in post-colonial times. On the whole, it seems better to adopt an inclusive approach to what constitutes the Atlantic Rainforest in this area.

Smith (1962), in his study on the origins of the flora of southern Brazil, pointed out that the numbers of species decreases from southeastern region to southern region (from the S of São Paulo to N of Rio Grande do Sul), and that the vegetation of the Paraguay river basin, with a gallery forest character, has apparently invaded southern Brazil via the Uruguay river and its tributaries,

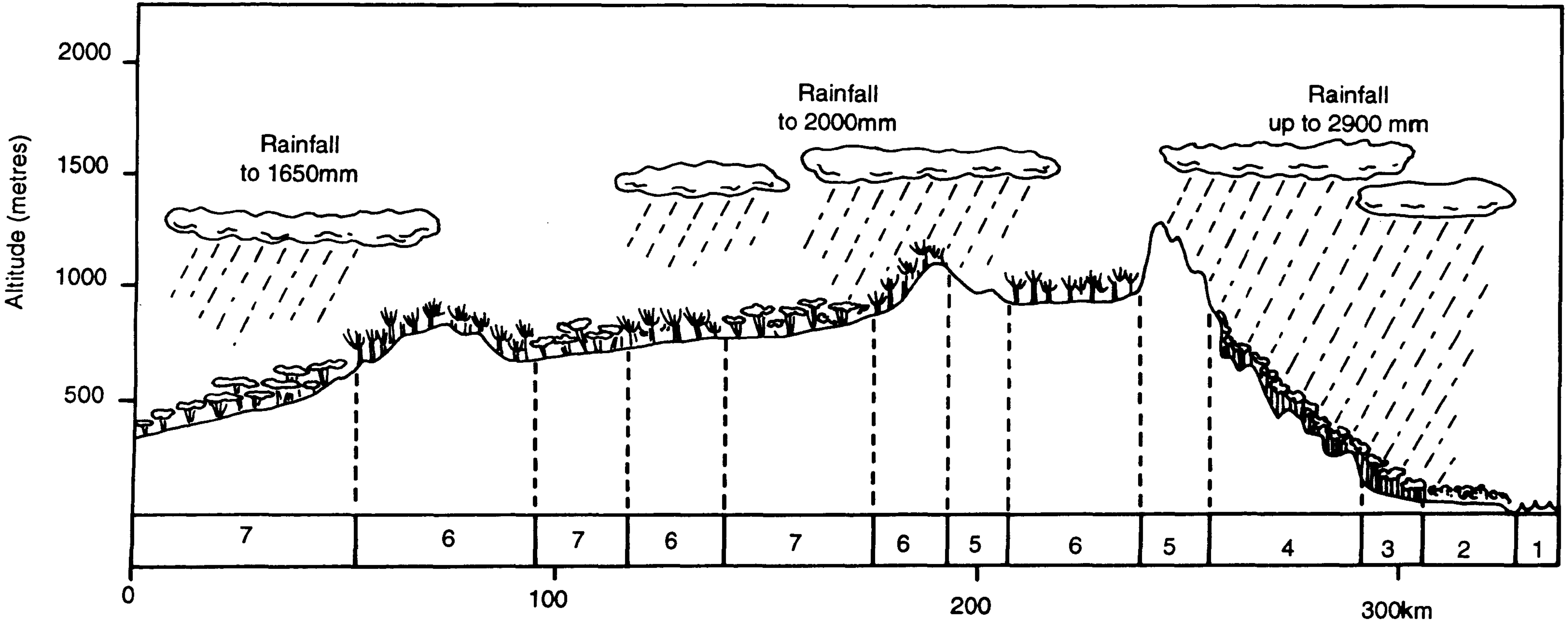


Figure 3.5. Diagramatic profile across the Atlantic Rainforest province in the Southern Sector (Parana State): 1) Atlantic Ocean; 2) 'restinga' and mangrove' 3) lowland wet forest; 4) montane wet forest; 5) high montane grassland; 6) *Araucaria* forest, and 7) mesophytic forests formation. Source: Maack (1981), modified.

crossed the planalto and entered the moist Atlantic forest formation. However, this scenario is not supported by distribution of bromeliad genera such as Vriesea, Tillandsia, Aechmea and Billbergia. The only genus which seems to have penetrated open areas of restingas and granitic outcrops of the Atlantic Rainforest province from the interior is Dyckia, with an distribution pattern from the Cerrado and Caatinga domain to the southern and southeastern regions of the coastal plain, as observed by Smith (1962), and Bromelia (personal observation) which presents a similar pattern to Dyckia. For the Bromeliaceae a small centre of endemism is found between the States of Santa Catarina and Paraná, with 54 taxa (35%) of a total of 155 that occur in the southern sector, representing 20% of the total Bromeliads that occur in the Atlantic Rainforest province (Appendix 1). The biggest concentration of bromeliads found in this sector occurs on the moist forest formation, with 84 taxa (54%), followed by mesophytic forests formation with 39 taxa (25%), restinga with 18 taxa (12%) and Araucaria forest with 14 taxa (9%).

CHAPTER 4. MATERIALS AND METHODS

4.1. STUDY AREAS

Field studies on the reproductive biology of a total of 35 species of Bromeliaceae were carried out in the Atlantic Rainforest Province of Rio de Janeiro State, during the period of December 1991 to January 1993.

Three studies areas (Figure 4.1), located at three altidudinal zones, were selected: I) Sea level - 120m, including restinga formation, mangrove, coastal granitic outcrops and lowland wet forest (Plate 4.2,a,b); II) 800 - 1500m with montane wet forest (Plate 4.1,a), and III) 1600 - 2000m in high montane grassland (Plate 4.1,b).

Area 1: Paraty, on the coast (from sea level at 120m of altitude). The vegetation in this area consists of restinga, coastal saxicolous communities of granitic outcrops either rising from the coastline and forming small islands offshore, and lowland wet forest. In this area the following species were studied:

Aechmea distichantha var. distichantha	-saxicolous on granitic outcrops
Dyckia pseudococcinea	-saxicolous on granitic outcrops
Neoregelia compacta	-saxicolous on granitic outcrops
Neoregelia marmorata	-saxicolous/epiphytic on granitic outcrops, restinga and mangrove
Nidularium billbergioides var. billbergioides	-epiphytic/terrestrial in lowland wet forest
Pitcairnia flammea var. flammea*	-saxicolous on granitic outcrops

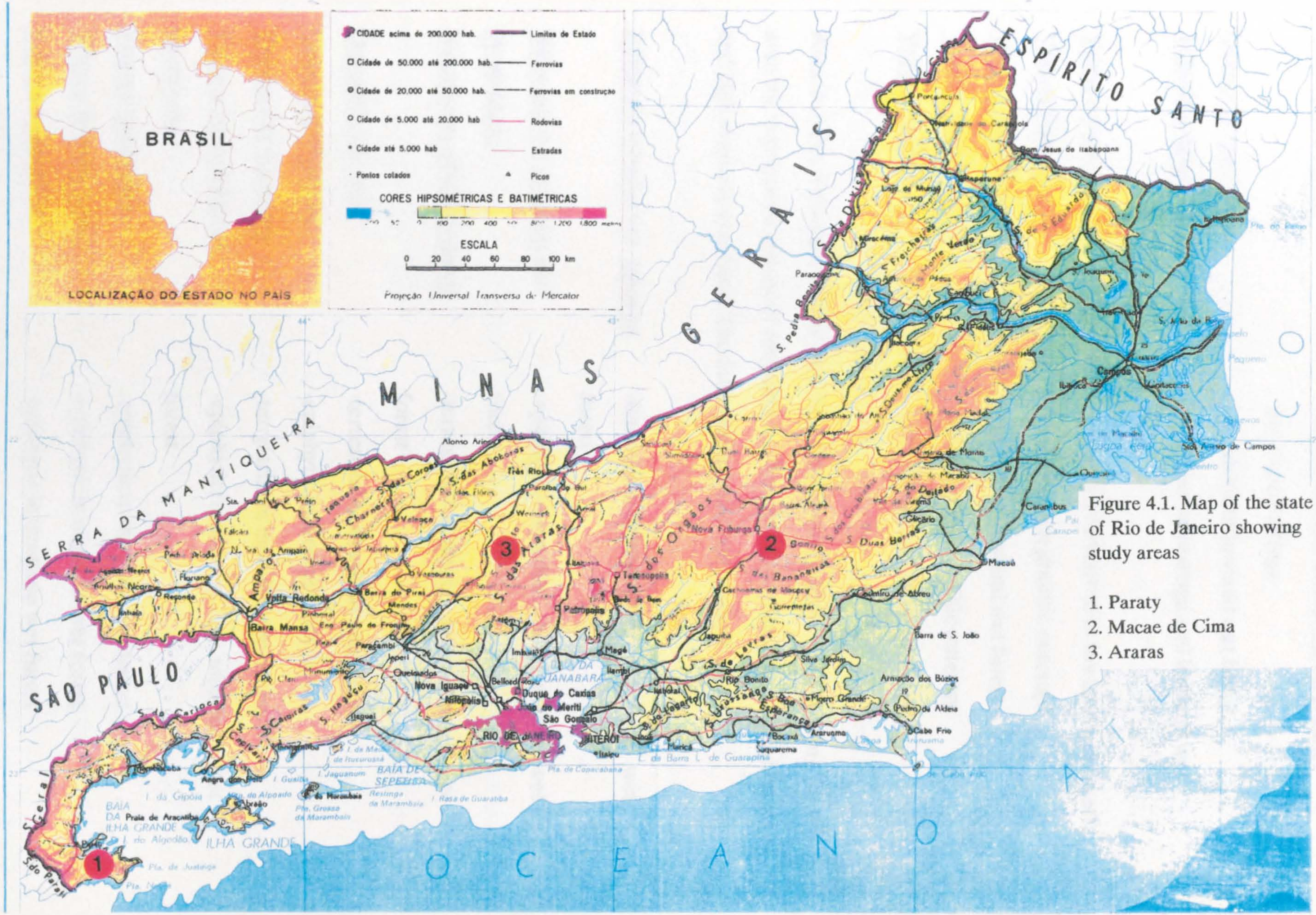


Figure 4.1. Map of the state of Rio de Janeiro showing study areas

1. Paraty
2. Macae de Cima
3. Araras

Quesnelia arvensis*	-saxicolous and terrestrial on grantic outcrops/restinga
Quesnelia marmorata	-epiphytic in lowland wet forest
Tillandsia stricta var. stricta	-epiphytic in restinga and lowland wet forest
Vriesea ensiformis var. ensiformis*	-epiphytic/terrestrial in lowland wet forest
Vriesea flammea	-saxicolous on granitic outcrops
Vriesea incurvata*	-epipytic in lowland wet forest
Vriesea neoglutinosa	-saxicolous on granitic outcrops
Vriesea regina*	-saxicolous on granitic outcrops

Area 2: Nova Friburgo, Macaé de Cima Ecological Reserve (900-1600m). In this area the vegetations consist of montane wet forest ('slope forest' and 'cloud forest') and high montane grassland. The following species was studied:

Billbergia amoena var. amoena	-terrestrial/epiphytic in montane wet forest
Billbergia pyramidallis var. pyramidallis	-epiphytic/terrestrial in montane wet forest
Nidularium scheremetiewii	-terrestrial/epiphytic in montane wet forest
Quesnelia lateralis*	-terrestrial in montane wet forest
Quesnelia liboniana	-epiphytic in montane wet forest
Vriesea altomacaensis	-terrestrial in montane wet forest
Vriesea bituminosa var. bituminosa*	-epiphytic/terrestrial in montane wet forest
Vriesea haematina	-epiphytic in montane wet forest
Vriesea heterostachys*	-epiphytic in montane wet forest
Vriesea hydrophora*	-epiphytic in montane wet forest

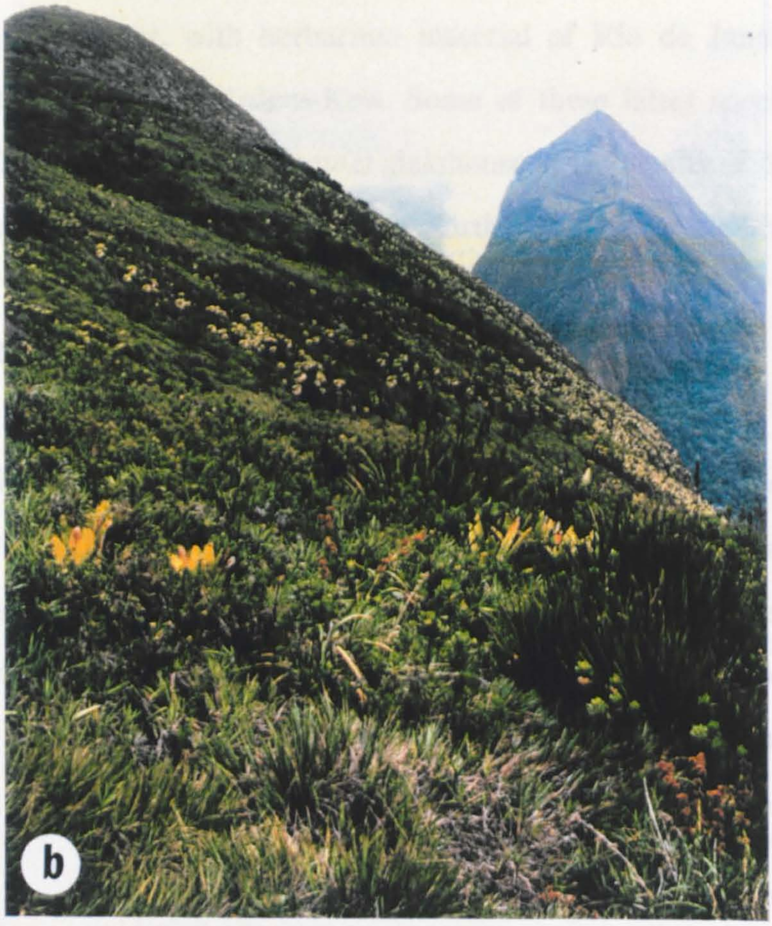
Vriesea imperialis*	-saxicolous in high montane grassland
Vriesea longiscapa*	-epiphytic/terrestrial in montane wet forest
Vriesea paraibica	-epiphytic in montane wet forest
Vriesea sparsiflora var. sparsiflora*	-epiphytic/terrestrial in montane wet forest
Vriesea vagans	-epiphytic in montane wet forest

Area 3: Petrópolis, Araras (between 800 - 1900m of altitude). The vegetation of this area consists of montane wet forest and high montane grassland. The following species was studied:

Aechmea fasciata var. fasciata	-epiphytic in montane wet forest
Billbergia pyramidallis var. pyramidallis	-terrestrial/epiphytic in montane wet forest
Pitcairnia flammea var. flammea*	-saxicolous in rocky streams of montane wet forest
Quesnelia augusto-coburgii	-saxicolous/terrestrial in montane wet forest
Vriesea atra var. atra	-saxicolous in high montane grassland
Vriesea ensiformis var. ensiformis*	-epiphytic in montane wet forest
Vriesea heterostachys*	-epiphytic in montane wet forest
Vriesea imperialis*	-saxicolous in high montane grassland
Vriesea longicaulis	-terrestrial in montane wet forest
Vriesea psittacina var. psittacina	-epiphytic in montane wet forest

Plate 4.1. (a) interior of the montane wet forest in Ecological Reserve of Macaé de Cima, Nova Friburgo, Rio de Janeiro State at 1100m; (b) view of high montane grassland in Petrópolis, at 1850m.


a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Just one species was studied in additional area of montane wet forest in Teresópolis, Serra dos Órgãos National Park (1100m of altitude). The object of this was to compare the two varieties of Pitcairnia flammea - var. flammea vs. var. pallida.

At these sites, 14 species were studied in some detail (starred) for their flowering phenology, pollination biology and breeding system, and natural fruiting success, and a further 21 species were studied for flowering phenology, and usually pollination biology, but with incomplete data for the breeding systems. When possible, populations of these species comprising a minimum of 30 individuals were selected.

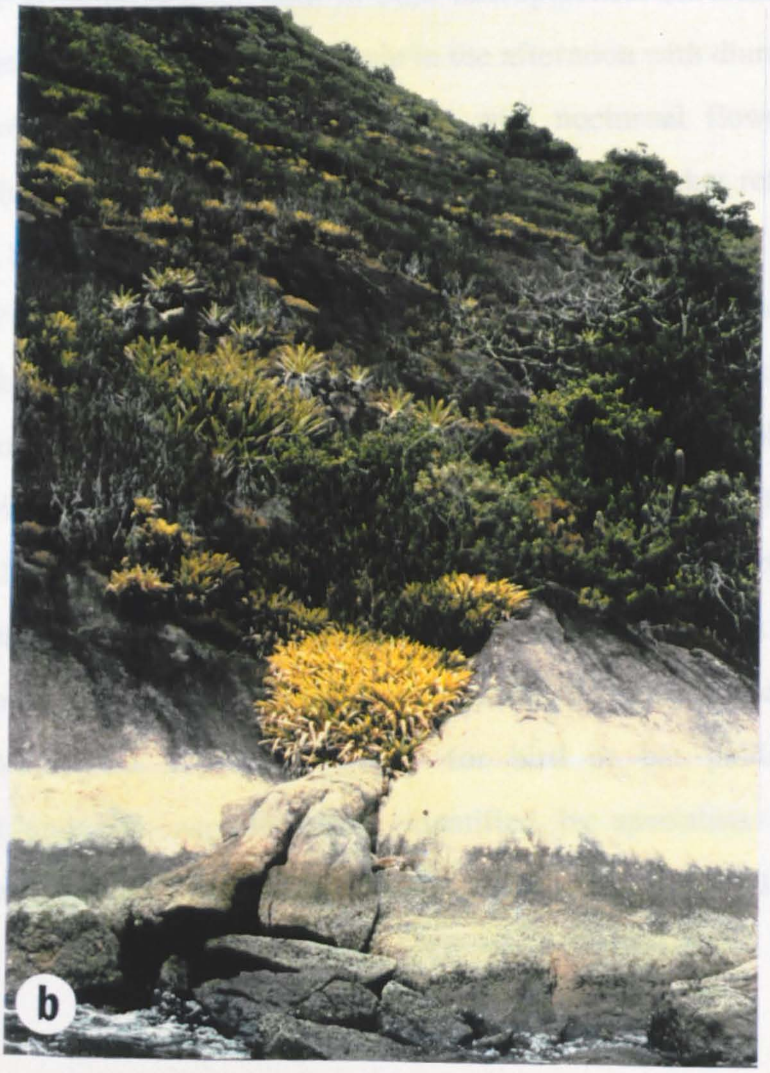
Voucher specimens of each species were collected and deposited in the herbarium of Rio de Janeiro Botanic Garden. A live collection was made of the almost all species studied and these were included in the Bromeliaceae collection of Rio de Janeiro Botanic Garden and some duplicate living material was donated to the Royal Botanic Garden-Edinburgh. Identifications were made by myself and checked when neccessary, with herbarium material of Rio de Janeiro Botanic Garden and Royal Botanic Gardens-Kew. Some of these latter specimens were temporarily cultivated in the experimental glasshouse at University of St. Andrews so that if they came into flowers they could be further studied for breeding system.

4.2. FLOWERING PHENOLOGY

The flowering period for each species was monitored by means of monthly or fortnightly observations on the populations, which were then adjusted in frequency as plants produced inflorescences, or flowers buds were evident. Initiation and end of flowering, together with peak flowering period (with 50% of individuals in the population in flower) were noted. Also the nature of the inflorescences, number of flowers in sample inflorescences, and number of flowers

Plate 4.2. (a) restinga forests and lowland wet forest in Paraty, at sea level; (b) granitic outcrops in Paraty, at sea level.


a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per inflorescence opening per day were also estimated. The timing of fruit maturation and seed release were also noted.

4.3. POLLINATION BIOLOGY

For each species, sample flowers were collected and flower structure studied by means of dissections. The phases of of floral anthesis were monitored in the field by tagging mature buds with cotton thread and accompanying the opening and longevity of individual flowers with repeated diurnal or nocturnal observations. Notes were also made on flower colour and any colour changes, scent, anther dehiscence and stigma position and condition, and photographs were taken of various stages.

Nectar production was sampled in flowers which had been protected from pollinator visits using 10μl, 20μl or 50μl micropipettes. Such samples were usually taken during the mornings, and again in the afternoon with diurnal flowers, and in the evening and again post-midnight with nocturnal flowers. Nectar concentration (sucrose equivalents) were estimated using a pocket refractometer (Bellingham & Stanley, 0-50%).

Field observations on the spectrum of animal/insect visitors to the flowers of each species were realized for 1-5 observation periods lasting from 30 minutes to 4 hours in order to establish the identity of the probable pollinator. For species with diurnal flowering the observation period started at 06:00h with the latest around 18:00h, and for nocturnal flowering from 16:00h to 03:00h. Flower visitors were photographed whenever possible and behaviour of main visitors was noted. Specimens of some flower visitors, were captured for identification using a standard entomological net or "mist-nets" for bird or bat pollinators. The hummingbirds and bats captured were identified by specialists of Zoology Department of National Museum of Rio de Janeiro and Rio de Janeiro Zoo.

Insects were also captured and were brought to the University of St. Andrews for identification.

In some cases, pollen was sampled from the body of bat or bird visitors using slides smeared with glycerol jelly and these were subsequently mounted and compared with reference slides of pollen for the species under study.

4.4. BREEDING SYSTEM

One advantage of working with Bromeliaceae species is that once flowers have been initiated in both epiphytic and terrestrial species, the plant can be uplifted and transferred to another site. Such plants can be established in pots in a coarse bark/humus "soil" medium, and with the leaf-water tanks maintained with water, the transplants will thrive and flowering proceed at a normal rhythm. This aspect of bromeliad biology was manipulated with a number of species so that plants individuals were transferred from their natural habitat and small artificial "populations" of 2-6 individuals were established in cultivation at my house in Araras. Such plants, with ready availability and access, facilitated hand pollination studies.

As plants of various species in such artificial transplant population came in flower, a series of hand self- and cross-pollinations were carried out. For such pollinations whole inflorescences were bagged in nylon fine mesh bags to exclude visitors, or sometimes, the whole plant was monitored in a pollinator free-chamber. Pollen was transferred to stigmas by removing a dehiscing anthers from a donor flower (self or another individual for cross) and dabbing the anthers on the stigma. Such experimentally pollinated flowers were tagged with a colour cotton thread and jeweller's tag indicating date of pollination. In species which showed dichogamous phases of anther-stigma development, such pollination were made when the stigma appeared wet and receptive. The index of self-incompatibility were calculated for 14 species (ISI= % fruit-set from self-pollination / % fruit-set from cross-pollination, sensu Bullock 1985). For comparison of the mean of penetrated ovules from hand-pollination treatments, a *t*-student test (Wardlaw, 1992) was applied for each time intervals.

Pistils from a subsample of such hand-pollinated flowers were fixed in FAA (90ml 70% ethanol:5ml glacial acetic acid: 5ml 40% formalin) at various time intervals (24, 48, 72, 96, 120, 144 and 168h after pollination) for studies of pollen growth, and the remaining flowers were monitored for fruit-initiation and development. Fixed pistils were subsequently studied for pollen germination on the stigma, pollen tube growth of the style, and ovule penetration in the ovary, using decolourized aniline blue staining and fluorescence microscopy (Leitz Laborlux 12 Microscope fitted with Ploemopak 2.5 fluorescence vertical illuminator and ultraviolet filter) according to the schedule by Martin (1959). Cut styles and pistils were softened in 8 M NaOH in an oven at 60°C for 15-20 mins, briefly rinsed with water, partially dissected in a droplet of 0.1% leuco-aniline blue stain, and mounted on a slide in this stain. Such preparation of softened stigma, style or ovary material could be flattened somewhat by gently tapping/pressing the coverslip. For the time intervals available with the pistils of each species, details of pollen germination, rate of pollen tube growth in the style, and incidence of ovule penetration were noted for selfed- vs. crossed-flowers, and recorded with a Pentax camera and using either black and white Agfapan 100 film or Ektachrome 150 (tungsten) colour film.

CHAPTER 5. RESULTS: CASE HISTORY STUDIES

This section presents the results of field and laboratory studies of the reproductive biology of 35 species of Bromeliaceae of the Atlantic Rainforest in Rio de Janeiro State, SE, Brazil.

Section A comprises case history studies for 14 species for which reasonable complete data is available concerning flowering phenology, pollination biology, natural fruit-set and breeding system (with results of hand self- vs. cross-pollinations in terms of fruit-set and analysis of post-pollination events by mean of fluorescence microscopy).

Section B gives data for further 21 species for which data is incomplete. For most of these species flower phenology and pollination biology were studied, but because of constraints of time, or insufficient individuals to create cultivated 'populations' at Araras, details of hand-pollination studies are usually restricted to selfings, and fruit-set data are lacking.

SECTION A:

5.1. Vriesea bituminosa Wawra var. bituminosa [Table 5; Figure 5; Plate 5.1,a,b]

MORPHOLOGY: Plant epiphytic or saxicolous with many leaves in a spreading rosette. Inflorescence simple, 50cm long, with many distichous flowers, completely covered with a very glutinous exudate; floral bracts inflated, fleshy and becoming very rugose on drying, greenish-brown with red spots and dark margins. Flowers spreading at anthesis, sepals green with dark margins, petals 6cm, exceeding the stamens, chestnut-reddish, bearing two large and acute appendages at base; filaments thickened toward the apex; stigma convolute-blade type.

DISTRIBUTION AND HABITAT: This species is found as saxicolous or epiphytic plants in the high montane grassland and montane wet forest of the southeastern sector of the Atlantic Rainforest province, between 1200-2200m, in Rio de Janeiro, São Paulo and Minas Gerais States. (also doubtfully occurring in Venezuela: Foster 2780, as cited in Smith & Downs, 1977). The species was studied in the Ecological Reserve of Macaé de Cima, Nova Friburgo, Rio de Janeiro State.

FLOWERING PHENOLOGY: The flowering period of Vriesea bituminosa var. bituminosa began in late December and finished in early February, with a marked synchrony among the individuals of the population of the study area. Mature fruits were present in early June (Figure 5).

The mean number of flowers per plant was 35 flowers (N=6) and this species opened 1-2 flowers per night per plant and the availability of the flowers was characterized as 'steady state' (Gentry, 1974).

POLLINATION BIOLOGY: V.bituminosa var. bituminosa is a night-blooming species, with the flowers beginning to open around 17:35h and with anthesis completed nearly 11 hours later. Anthesis in Vriesea bituminosa var. bituminosa showed dichogamy with marked protandry. In the early hours of the anthesis, the stigma is not receptive and is located at the same height of the apex of anthers, but the style gradually extended to reach 8mm above the apex of the anthers, some 4 hours later, at which time the stigma was receptive (Table 5.1.1).

When the buds are young they lie along the rhachis and gradually move downward and become spreading but not secund. When in bud the corolla is pale-chestnut, changing to chestnut-reddish during the anthesis. The whole inflorescence presents a very strong, glutinous and sticky substance on the surface

Table 5.1.1. Sequence of the anthesis of Vriesea bituminosa var. bituminosa (N=8).

TIME	COROLLA	STAMENS	STYLE	REWARD
16:00	corolla beginning to open; petals castaneous	stamens included, not releasing pollen	stigma at the same height at the apex of the anthers, dry, not receptive	no nectar
17:20	corolla open with petals straight; petals castaneous, reddish at apex and margins	apex of the anthers at the same height of the petals apex; beginning to release pollen	stigma 2-3mm above the apex of the anthers, not receptive, dry	nectar
20:30	corolla open with apex of the petals slightly recurved, petals castaneous reddish	apex of the anthers exposed by the recurved apex of the petals	stigma 6-7mm above the apex of the anthers, becoming receptive and wet	nectar
01:00	corolla open	anthers releasing pollen	stigma 8mm above the apex of the anthers, receptive	nectar
04:00	corolla closing	anthers empty; filaments becoming flaccid	stigma dry, not receptive	no nectar

of the bracts, rachis, sepals and even outer surface of the petals, such that many insects of small and medium size are imprisoned on surface of the inflorescence.

The septal nectaries have three slits localized in the gynoecial sutures. The petal appendages are acute, embracing the style, and partitioning off a lower intrafloral chamber where the nectar is released.

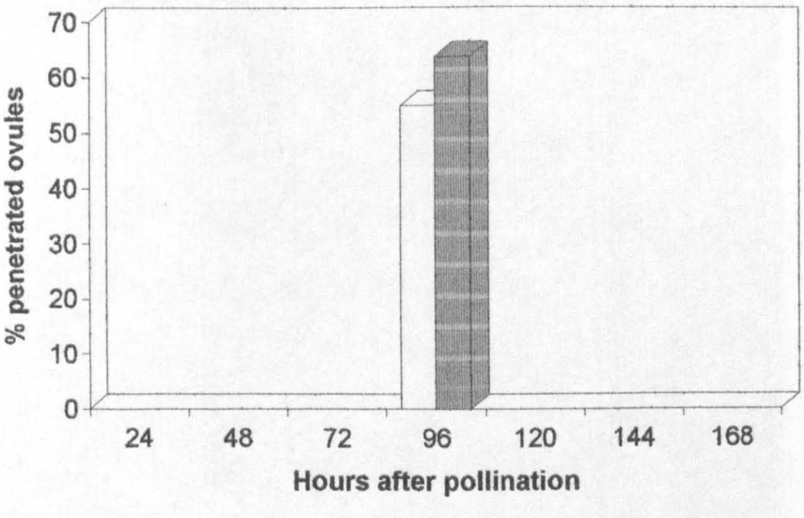
The sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The volume of nectar in a single flower of Vriesea bituminosa var. bituminosa at 23:00h was 207μl (N=1), and the mean concentration of sucrose equivalents was 13.4% (N=6, SD±1.6, Range 12-18%).

No pollinators were observed despite observations for several hours on various nights. This species is most likely to be pollinated by small bats and/or nocturnal hawkmoths.

BREEDING SYSTEM: An experimental population comprising four individuals which were collected in the early stage of flowering from two different natural populations was cultivated in Araras. The hand-pollinations were performed with previously bagged flowers (N=18). A subsample of hand-pollinated pistils from different treatments were fixed at 96h after pollination (Figure 5.1). Fruit-set from the remaining hand-pollinated flowers was followed until maturation (Table 5.1.2).

In both self- and cross- pollinated pistils the pollen grains germinated prolifically on the stigma and at 96 hours the self- and cross-pollen tubes had reached the ovary, at which time the selfed pistils showed strikingly more penetrated ovules than crossed ones. However, the sample size for crossed pistils was small, due the fact that some fixed material was found to be infected with fungus in the stigma, but the percentage of fruit-set from hand-pollination treatments of the artificial population for which mature fruits were collected, showed a high percentage of fruit-set from crossed pistils (see Table 5.1.2).

Figure 5.1. - Vriesea bituminosa var. bituminosa: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



96h- SP: N=6, range 39.9-94.7%
CP: N=4, range 23.4-87.2%
P>0.05

Plate 5.1. (a) flower of Vriesea bituminosa var. bituminosa; (b) pollen tubes penetrating the micropyle of ovules at 96 h after self-pollination (scale bars = 100μm).

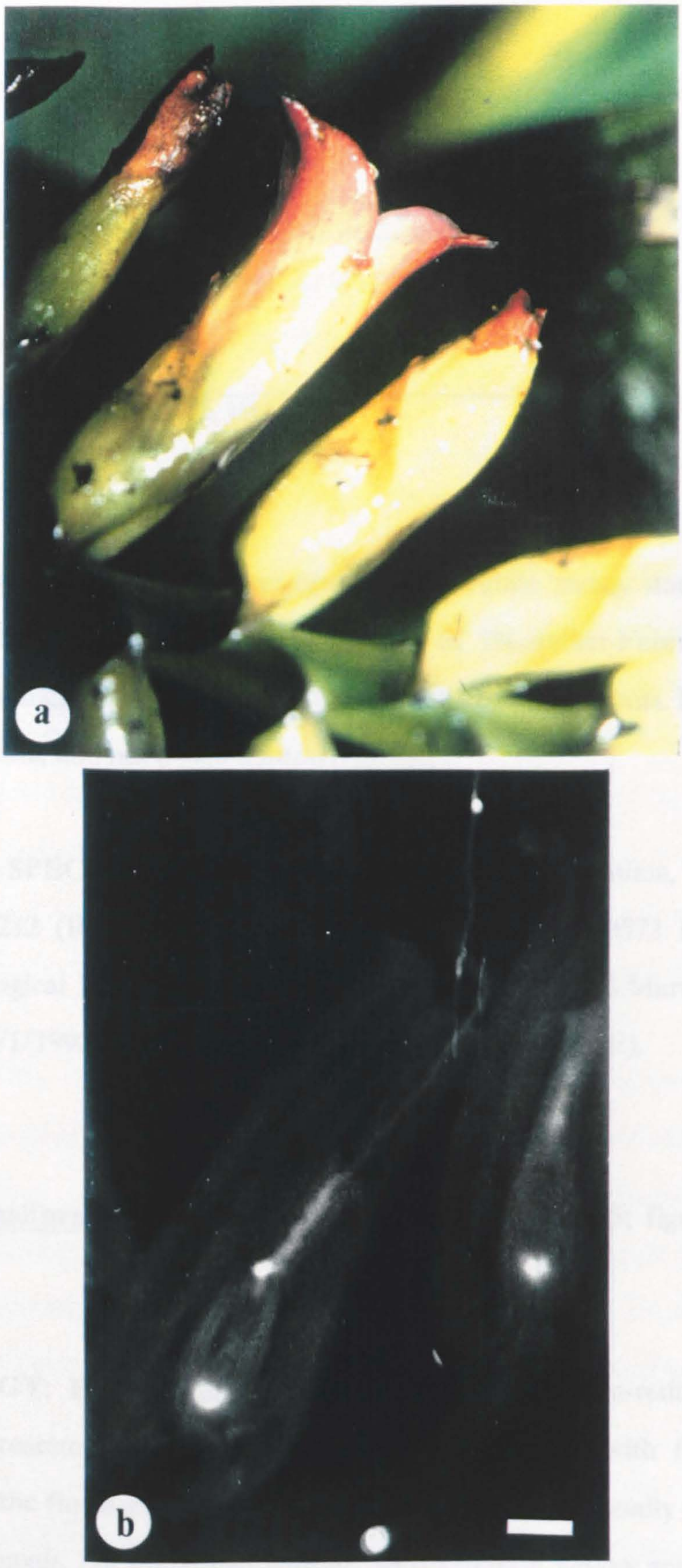

a
b

Table 5.1.2. Results of experimental hand-pollinations treatments with Vriesea bituminosa var. bituminosa fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	83.3% (5/6)
selfs	66.6% (4/6)
natural fruit-set	-
ISI*	0.79

* Index of self-incompatibility (Bullock, 1985).

SUMMARY: Vriesea bituminosa var. bituminosa exhibits 'steady state' flowering phenology (Gentry, 1974), during the months of December-February. It has nocturnal flowering, and is most likely to be pollinated by small bats. It appears to be self-compatible, and has a high natural fruit-set.

BOTANICAL SPECIMENS: Rio de Janeiro State: Itatiaia, 01/I/1977, G.Martinelli 3212 (RB); Petrópolis, 26/III/1967, E.Pereira 10572 (HB); Nova Friburgo, Ecological Reserve of Macaé de Cima, 20/V/1987, G.Martinelli 12043 (RB); idem, 14/I/1992, G.Martinelli 14701 (RB), cultivated RB, E).

5.2. Vriesea ensiformis (Vell.) Beer var. ensiformis* [Table 5; figure 5; Plate 5.2,a,b]

MORPHOLOGY: Epiphytic plants with leaves green and green-reddish forming a funnelform rosette. Inflorescence simple, many-flowered, with floral bracts spreading with the flowers at anthesis and exposing the rachis, usually equalling or exceeding the sepals, but sometimes shorter. Sepals elliptic, yellow and sometimes reddish to the base; petals yellow, bearing two large appendages at base. The stamens are exserted and the stigma is of the convolute-blade type.

* Taxonomic observation: Smith & Downs (1977) in their monograph of the Bromeliaceae/Tillandsioideae, maintained Vriesea ensiformis (Vell.) Beer and Vriesea gradata (Baker) Mez, as two different species based on differences in size of floral bracts in relation to that of the sepals (V.gradata exceeding vs. V.ensiformis not exceeding the sepals). In the two populations monitored in two different study areas (Paraty and Petrópolis) individuals were found which present a gradation in this sepal character asestablished by Smith & Downs (1977). Moreover, in a same inflorescence floral bracts can reach 53mm in the flowers at the base of inflorescence, thus exceeding the sepals, whilst the bracts of flowers in the upper-half of the inflorescence were of 37-42mm, with the apex of the sepals exposed. Curiously, Fountoura et al.(1991) in a check-list of the Bromeliaceae from Rio de Janeiro State, cited plants of the same areas and same populations which I monitored as two different taxa: Araras, Petrópolis: G.Martinelli 1640 (RB); Paraty, Paratimirim: Carauta 2252 & al. (GUA) and A.Costa 91 & al. (RB) as V.gradata, and D.Sucre 2568 & P.I.S.Braga (RB); D.Sucre 4875 & P.I.S.Braga (RB) as V.ensiformis var. ensiformis; Moreover, the cross-pollination experiments were made between individuals from the populations at Paraty and Petrópolis, and no differences or pollen rejection were found. For the present study, therefore, "V.gradata" is treated as V.ensiformis var. ensiformis.

DISTRIBUTION AND HABITAT: This species is found as an epiphyte in moist forest formations of eastern, southeastern and southern sectors of the Atlantic Rainforest province, and also in 'Restingas', occurring from sea level to 1100m, in the States of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná and Santa Catarina. The species was studied at two sites: (a) Araras, Rio Capoeirão, Petrópolis, and (b) Paratymirim, Paraty, both in Rio de Janeiro State.

FLOWERING PHENOLOGY: Vriesea ensiformis var. ensiformis has almost the same flowering period in both areas of study, flowering massively during the months of December and January, with a definite peak of flowering in January. Mature fruits occur at the beginning of March (Figure 5).

The mean number of flowers per inflorescence was 16 (N=16). Flowers at the base of the inflorescence are the first to open such that flowering occurs in a ascending sequence. Vriesea ensiformis var. ensiformis is a day-blooming species and the flowers begin to open around 06:00h and close some 12 hours later. The complete sequence of the anthesis is showed in the Table 5.2.1.

POLLINATION BIOLOGY: Anthesis of V.ensiformis var. ensiformis demonstrated dichogamy with a marked protandry. In the early hours of anthesis, the stigma is not receptive and is located only 2mm above the apex of the anthers, but the style gradually extends so the stigma is eventually located some 10mm above the anthers, some four hours later, at which time the stigma is receptive (see Table 5.2.1). The availability of the flowers was characterized as 'steady state (Gentry, 1974), with only one to two flowers opening per day.

The most important visual advertisement for the pollinator in this species seems to be the colour of the floral bracts which vary between full red to red with yellow or green margins and apex. The flower is largely hidden by the floral bracts, with only the upper part of the petals showing and the exserted anthers and stigma. When the inflorescence is young the buds and the floral bracts are contiguous with the rachis, with the inferior part of the floral bracts covered by the adjacent inferior bract. The position of the bracts and the buds gradually changes during the development of the buds through the anthesis, and during the anthesis the flowers and the bracts becoming spreading from the rachis, and exposing an evident space between them, in a sequence from the base to the apex of the inflorescence. Generally, the last 3-4 flowers of the apex of the inflorescence are abortive.

Table 5.2.1. Sequence of anthesis of Vriesea ensiformis var. ensiformis (N = 12).

TIME	COROLLA	STAMENS	STYLE	REWARD
06:00	corolla beginning to open	anthers not releasing pollen, at same height of the petals	stigma at the same height at the apex of the anthers; dry, not receptive	beginnin to release nectar
07:00	corolla open with the petals recurving at apex and exposing the anthers	anthers releasing pollen and filament developing and changing the position and joining to one sid, with the longitudinal dehiscence concerned for one side	stigma 2mm above tha apex of the anthers; dry, not receptive	nectar
10:00	corolla open	anthers releasing pollen, 6mm above the petals	stigma 6-8mm above the apex of the anthers, becoming wet and receptive	nectar
11:00	corolla open	anthers releasing pollen	stigma 10mm above the apex of the anthers; receptive	nectar
13:00	corolla open	anthers releasing pollen	stigma 10mm above the apex of the anthers, receptive	nectar
18:00	corolla closing	stamens dry, anthers empty	stigma dry, not receptive	no nectar

The septal nectaries have three slits near the apex of the ovary. During anthesis the apex of the petal appendages embrace the base of the style, cutting off a lower chamber where the nectar is released.

The volume and sugar concentration of nectar was measured in previously bagged flowers. Nectar in V.ensiformis var. ensiformis is available from the time the corolla opens, with the mean volume of nectar 32.4μl (N=3, SD±5.98, range 28-42.9μl), and the mean of concentration of sucrose equivalents of 21.9% (N=32, SD±4.68, Range 16-30%).

Observations on natural pollination were carried out in both populations (Paraty, at sea level and Petrópolis, at 900m of altitude), and in both the visitors were hummingbirds. At the Petrópolis population, the hummingbird Melanotrochilus fuscus was the only visitor observed, and although this hummingbird species presented a sequential pattern of visits, the frequency of visits was relatively low. At Paraty two hummingbirds were observed, Leucochloris albicollis and Amazilia fimbriata, although neither presented a definite pattern of visits or frequency, or territorialist behaviour, and so both species could be opportunistic visitors, although Leucochloris albicollis certainly touched the stigma of V.ensiformis flowers in its visits. No other visitors of the flowers of this species was observed.

BREEDING SYSTEM: An experimental population comprising nine individuals which were collected from the two different natural populations was cultivated in Araras. Self- and cross-pollination were carried out with these plants (N=37). A subsample of hand-pollinated pistils from different treatments as fixed at 72h and 96h post-pollination for subsequent analysis under fluorescence microscopy. Fruit-set from the remaining hand-pollinated flowers was followed until maturation, and an estimate of the natural fruit-set was obtained from tagged flowers (N=40) from different plants of both natural populations (Table 5.2.2).

For both self- and cross- hand-pollinated flowers pollen germinated prolifically on the stigma and a mass of pollen tubes was evident in the style in each case. Within the ovaries, both self- and cross pollen tubes achieved numerous ovule penetrations, but at both 72 and 96h cross-pollen tubes showed rather higher levels of ovule penetration (Figure 5.2.1). The fruit-set percentage from natural population was relatively low, with 65% of the tagged flowers forming fruits (see Table 5.2.2).

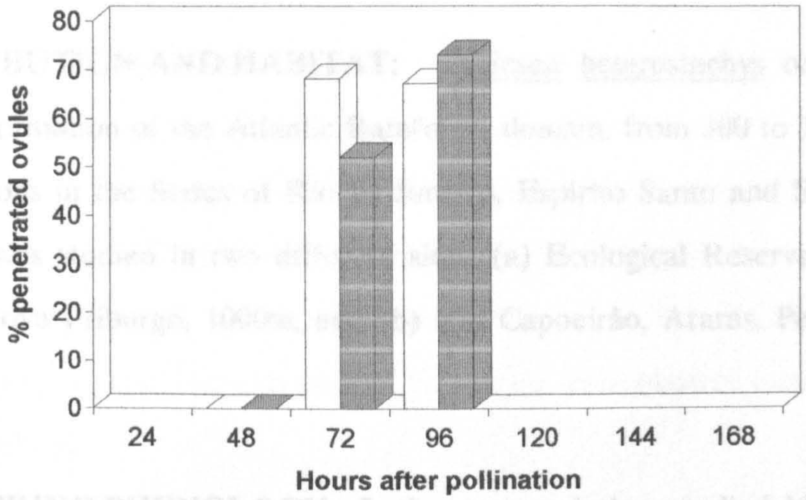
SUMMARY: Vriesea ensiformis var. ensiformis exhibits 'steady state' flowering phenology (Gentry, 1974), during the months of December, January and February. It has a diurnal flowering, and is hummingbird-pollinated, being visited by Leucochloris albicollis, Melanotrochilus fuscus and Amazilia fimbriata in the study areas. It appears to be self-compatible, and has a relatively low natural fruit-set.

Table 5.2.2. Results of experimental hand-pollination treatments with Vriesea ensiformis var. ensiformis fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	33.3% (3/9)
self	20% (2/10)
natural fruit-set	65% (26/40)
ISI	1.66

BOTANICAL SPECIMENS: Rio de Janeiro State: Araras, Petropólis, Rio Capoeirão, 17/IV/1977, G.Martinelli 1640 (RB); idem, 25/III/1968, D.Sucre 2568 & P.I.S.Braga (RB); idem, 12/IV/1992, G.Martinelli 14683 (RB; cultivated RB, E); Paraty, Paratimirim, 21/XII/1976, P.Carauta 2252 & al. (GUA); idem, 15/06/1987, A.Costa 91 & al. (RB); idem, 11/IV/1969, D.Sucre, 4878 & P.I.S.Braga (RB); idem, 12/XII/1992, G.Martinelli 14721 (RB, cultivated RB, E).

Figure 5.2. Vriesea ensiformis var. ensiformis: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



72h- SP: N=5, range 45.9-56.7%
CP: N=4, range 61.5-74.6%
$P<0.05$
144h- SP: N=3, range 71-75%
CP: N=3, range 51.5-77.9%
$P>0.05$

5.3. Vriesea heterostachys (Baker) L.B.Smith [Table 5; Figure 5; Plate 5.2,c,d]

MORPHOLOGY: Epiphytic plants, up to 45cm high with the inflorescence extended. Leaves dense, green or reddish, forming a dense rosette. The scape is erect or ascending, with bracts densely imbricate. The inflorescence is simple and few flowered, the floral bracts 4-5cm, and with a very sharp, curved keel, 4-5cm long, orange-reddish with yellow margins, exceeding the sepals. The flowers are short-pedicellate with sepals c. 38mm; petals c. 45mm, yellow with a green apex, bearing two appendages at base; stamens in two lengths, exserted and the stigma convolute-blade type.

DISTRIBUTION AND HABITAT: Vriesea heterostachys occurs in moist forests formation of the Atlantic Rainforest domain, from 300 to 1300m in small populations in the States of Rio de Janeiro, Espírito Santo and São Paulo. The species was studied in two different sites: (a) Ecological Reserve of Macaé de Cima, Nova Friburgo, 1000m, and (b) Rio Capoeirão, Araras, Petrópolis, 900m altitude.

FLOWERING PHENOLOGY: In the two populations studied, V. heterostachys presented different periods of flowering: the population of the Ecological Reserve of Macaé de Cima flowered during the months of November-December, whilst the population at Rio Capoeirão the flowered between January-February. Fruiting, in these two populations occured between February and April, respectively (Figure 5).

In both populations, the individuals presented largely synchronous flowering with 82 individuals flowering in the Ecological Reserve of Macaé de Cima, and 60 individuals in the population at Rio Capoeirão.

The average number of flowers per inflorescence was 10 (range 8-14; N = 13). Only one flower opens at a time in each inflorescence, lasting one day and with an interval of 2-3 days (rarely four) between subsequent flowers in the same inflorescence. Flowering thus falls into the 'steady state' type (Gentry, 1974). Flowering in V.heterostachys is diurnal, and flowers begin to open at c. 06:00h and show protandry (Table 5.3.1).

POLLINATION BIOLOGY: The dichogamous flowers of Vriesea heterostachys showed marked protandry. In the beginning of the anthesis, the stigma is situated at the same height as the anthers, but elongation of the style over a period of 4-5 hours results in the stigma being exserted by c. 10mm by the time it is unfolded, wet and receptive.

The septal nectaries are inferior, with three slits at the level of the apex of the ovary. During anthesis the petal appendages contact the base of the style and forming an intrafloral lower chamber, where the nectar is collected.

The nectar was present at the time of opening of the flowers (see Table 5.3.1) and was measured in previously bagged flowers. The mean concentration (sucrose equivalents) was 27.4% (N = 14, SD ± 3.32, range 20-31%). No changes in sugar concentration of the nectar were observed during the period of the anthesis.

The inflorescence of this species seems to be the most important attractive factor to the hummingbirds, with its bright orange-reddish and yellow floral bracts and yellow and green petals. The calyx and more than half of the corolla are hidden inside the bracts, so that only the apices of the petals are exposed together with the stigma and the anthers.

The only pollinator of V.heterostachys was the hummingbird Leucochloris albicollis, which was observed only at the population of Rio Capoeirão, which contained 56 plants. The time of duration of each visit was less than 1.5s and the interval between each visit to the same flower of the eight

Table 5.3.1. Sequence of anthesis of Vriesea heterostachys (N=32).

TIME	COROLLA	STAMENS	STYLE	REWARD
06:00	opening	three highest stamens with anthers liberating pollen	stigma at same height of the base of anthers of the highest stamens, dry, not receptive	nectar
07:00	open	three highest stamens with anthers liberating pollen	stigma at the lenght of the middle of anther of the highest stamens; dry, not receptive	nectar
09:00	open	all anthers releasing pollen	stigma 2mm above the apex the anthers of the highest stamens; dry, not receptive	nectar
10:00	open	anthers releasing pollen	stigma 4mm above the apex of anthers of the highest stamens; wet, receptive (?)	nectar
12:00	open	anthers releasing pollen	stigma varying between 7-10mm above the apex of anthers of the highest stamens; wet, receptive	nectar
16:00	open	anthers almost empty	stigma receptive	nectar
19:00	petals dry	stamens dry	stigma dry	no nectar

monitored individuals was between 20-60 minutes, during which intervals the hummingbirds visited other individuals of the population or perched nearby the population. The visits begin around 06:00h as the flowers open, and continued throughout the day until just after sunset, around 18:20h. No other visitors were observed at the flowers of this species. Leucochloris albicollis seems to be the effective pollinator of Vriesea heterostachys in the area of study, touching the anther and stigma during its visits.

BREEDING SYSTEM: An experimental population consisting of 13 individuals which were collected from both natural populations was cultivated in Araras. A total of 57 flowers were used in hand self- and cross-pollinations.

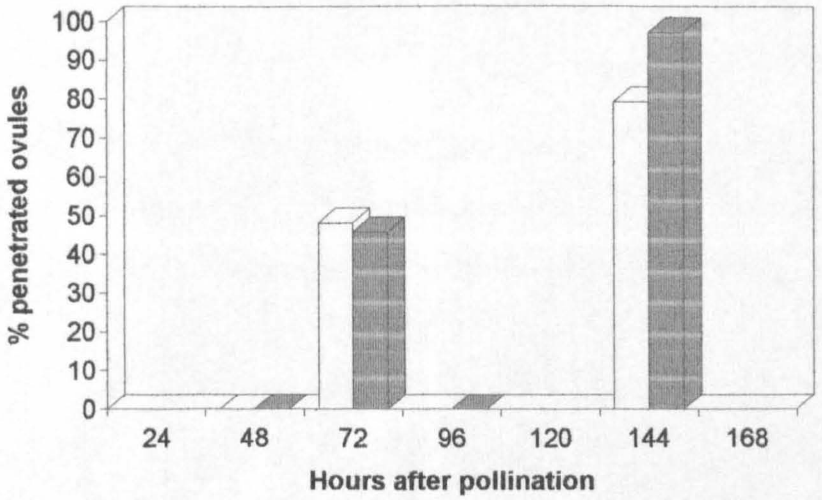
Cross- and self-pollen grains germinate prolifically on the stigma and a mass of pollen tubes grow down the style in each case. Cross-pollen tube growth is significantly more extensive in styles fixed at 24 hours, but by 48 hours both cross- and self-tubes have reached the ovary. Cross-pollen tubes have achieved higher levels of ovule penetration in pistils fixed at 72 hours but by 144 hours c. 80-90% of all ovules have been penetrated in both cases, although mean % penetration were actually higher in selfed pistils at this time (Figure 5.3.1).

Table 5.3.2. Results of experimental hand-pollinations treatments with Vriesea heterostachys fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	66.7% (4/6)
selfs	60% (6/10)
natural fruit-set	64% (32/50)
ISI	0.89

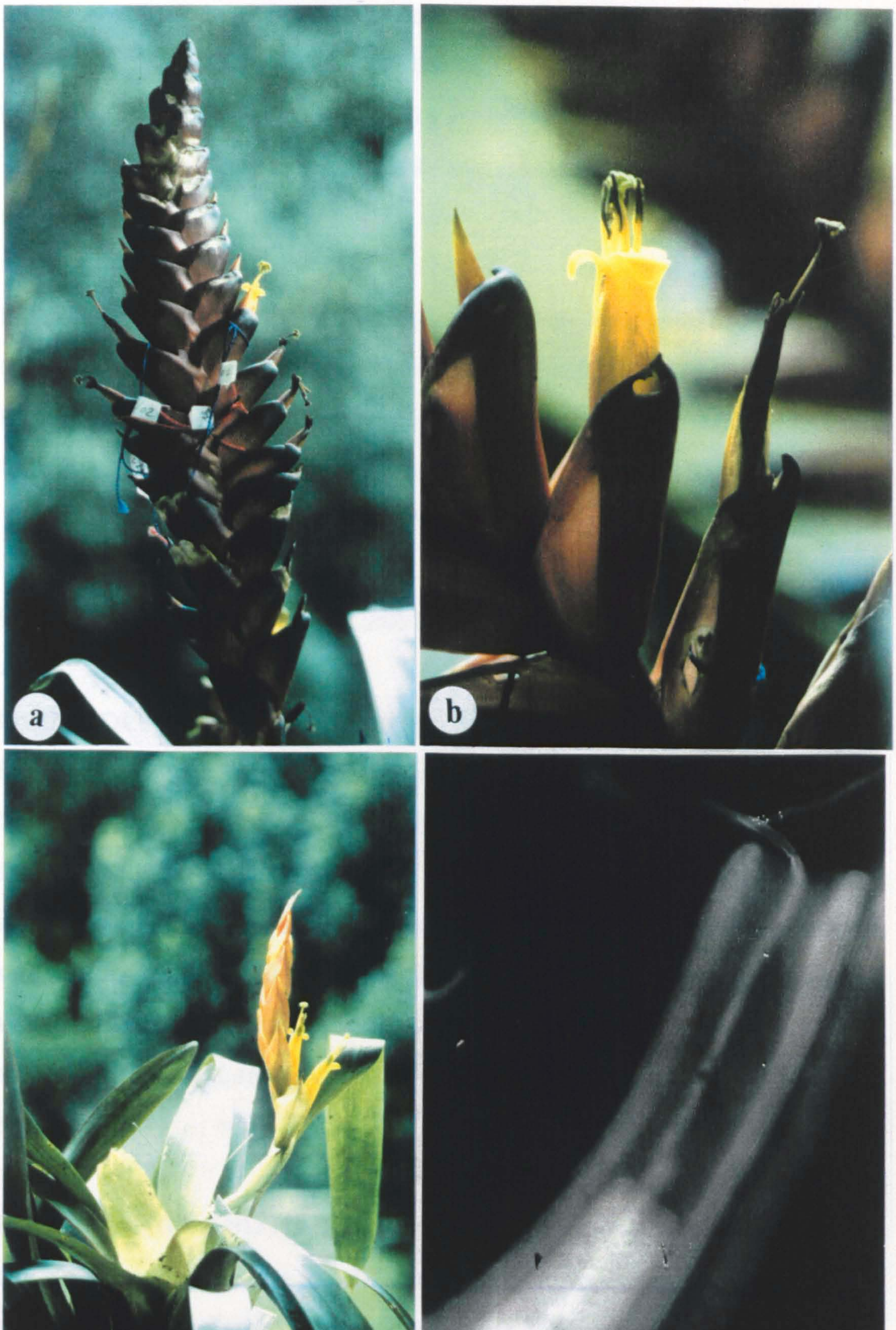
SUMMARY: Vriesea heterostachys exhibits 'steady state' flowering phenology (Gentry, 1974) despite the fact that both studied population occurr at more or less

Figure 5.3. Vriesea heterostachys: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



72h- SP: N=8, range 25.1-82.2%
CP: N=7, range 41.4-86.3%
P>0.05
144h- SP: N=3, range 74.2-84.1%
CP: N=1

Plate 5.2. (a) inflorescence of Vriesea ensiformis var. ensiformis; (b) flower detail; (c) inflorescence of Vriesea heterostachys; (d) pollen tube penetrating the ovule of V. heterostachys at 144 h after self-pollination (scale bars = 100μm).


a
b
c
d

the same altitude, one population flowering during the months of November-January and the other in January-March. It has diurnal flowering, and is hummingbird pollinated, being visited by Leucochloris albicollis in the study area. This species appear to be self-compatible with fruits developing both for cross- and self-pollination.

BOTANICAL SPECIMENS: Rio de Janeiro: Petrópolis, Araras, Maria Comprida, 04/XI/1975, G.Martinelli 851 (RB); idem, 23/III/1968, D.Sucre 2578 & P.I.S.Braga 419 (RB); Nova Friburgo, Ecological Reserve of Macaé de Cima, 18/X/1992, G.Martinelli 14681 & D.Miller (RB; cultivated RB, E).

5.4. Vriesea hydrophora Ule [Table 5; Figure 5; Plate 5.3,a,b]

MORPHOLOGY: Plants epiphytic with leaves to 1m, green, and forming a funnelform rosette. Scape erect with scape-bracts green and enfolding the scape. The inflorescence is densely paniculate, to 1.40m high, with branches to 20cm, densely 14-16 flowered. Floral bracts usually erect and not secund with the flowers, slightly exceeded by the sepals, carinate, and lustrous greenish-yellow. Flowers subspreading, secund, with a short pedicel; sepals greenish-yellow; petals ligulate, slightly exceeding the sepals, yellow, bearing two lanceolate appendages at base; stamens are included, filaments thickened toward the apex and stigma convolute-blade type.

DISTRIBUTION AND HABITAT: Vriesea hydrophora is a narrow endemic species of the montane wet forest, between 800-1100m, in the southeastern sector of the Atlantic Rainforest province, in the State of Rio de Janeiro, where just two populations are found. This species is found as epiphytic in the highest trees at the margins of streams. The species was studied in the Ecological Reserve of Macaé de Cima, Nova Friburgo.

FLOWERING PHENOLOGY: The development of the scape of Vriesea hydrophora begins in September, with the first flowers opening in December, and flowering cease in early March. Mature fruits occurs in early May (Figure 5).

The mean number of flowers per inflorescence was 112 (N=4) and the mean of flowers which opened daily per plant was 4 (N=11). The species is night-blooming and the flowers begin to open around 17:00h from a small aperture at the apex of the corolla, with the aperture gradually expanding until completely opened. The apex of each petal is slightly recurved. The anthers are included within the corolla, and only the apex of the anthers appears to be exserted due the recurved apex of the petals. The anthers begin to release pollen as the corolla opens but the stigma, which is placed at the same height as the apex of the anthers at this time, is not receptive, and only become so some four hours later by which time it is exserted some 5mm above the apex of the anthers (Table 5.4.1).

POLLINATION BIOLOGY: Anthesis in Vriesea hydrophora demonstrated a clear dichogamy with a marked protandry. The inflorescence is green but with a very lustrous surface to the bracts, which reflects the light, and this feature, together with the yellow petals and particularly the marked odour of the flowers, seems to be the most important advertisement to the pollinators. The inflorescence is very wet with a relatively sticky liquid on the surface of the bracts of the inflorescence which drips from them during anthesis. The flowers change their position from being contiguous to the rhachis when in bud, to upwardly secund during anthesis.

The septal nectaries have three slits located in the gynoecial sutures, and the petal appendages are lanceolate and embrace the style, thus cutting off a lower floral chamber, where the nectar is released.

Table 5.4.1. Sequence of anthesis of Vriesea hydrophora (N = 12).

TIME	COROLLA	STAMENS	STIGMA	REWARD
17:00	corolla opening; petals straight	stamens included and not releasing pollen	stigma dry, at the same height of the apex of the anthers; not receptive	nectar available
17:50	corolla open; apex of the petals recurved	apex of the anthers excluded from the recurved petals; releasing pollen	stigma dry, not receptive; 1-2mm above the apex of the anthers	nectar available
19:00	corolla open	anthers releasing pollen	stigma dry, not receptive; 3-4mm above the apex of the anthers	nectar available
21:00	corolla open	anthers releasing pollen	stigma wet, receptive; 4-5mm above the apex of the anthers	nectar available
02:00	corolla open	anthers becoming empty	stigma becoming dry; not receptive (?)	no nectar
03:30	corolla closing	anthers empty	stigma dry, not receptive	no nectar

The nectar of Vriesea hydrophora was available as the flowers open, with the maximum volume of nectar measured in a single flower of 90.8μl. The mean of concentration of sucrose equivalents was 13% (N = 13, SD ± 2.25, range 7-15%) and variable from flower to flower.

Despite several hours of observations on various different nights, no visitors were observed at the flowers of Vriesea hydrophora. The species is most likely pollinated by small bats or nocturnal moths.

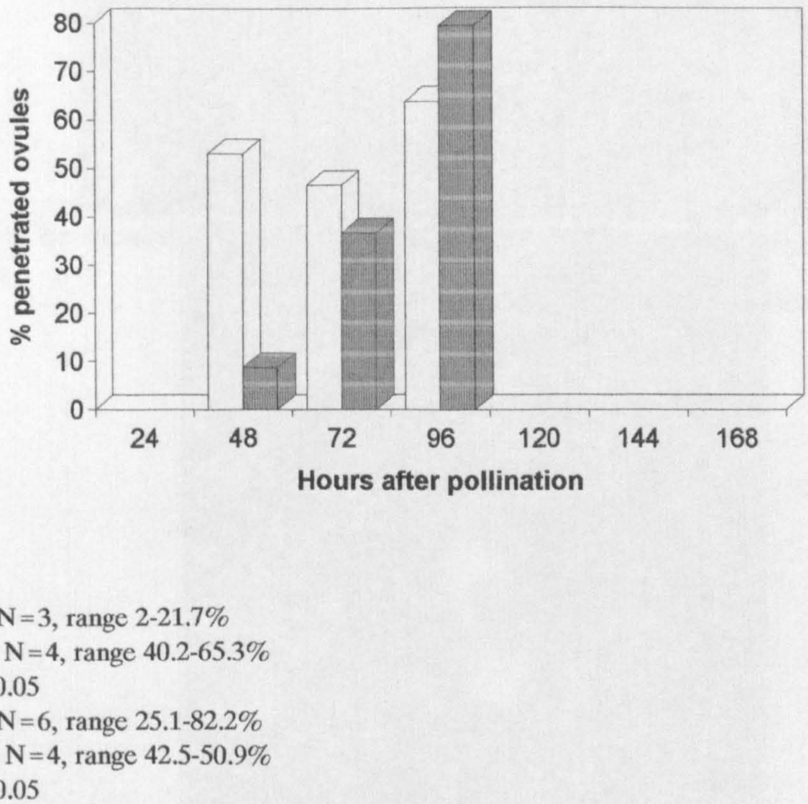
BREEDING SYSTEM: An experimental population was created with a sample of five individuals which were cultivated in Araras. The hand-pollinations were performed on a total of 57 flowers but only one sample of pistils was fixed at 72 hours (Figure 5.4.1). The fruit-set percentage from hand-pollination treatments of the transplanted population for which mature fruits were collected and the ISI (Bullock, 1985) are showed in the Table 5.4.2.

SUMMARY: Vriesea hydrophora exhibits 'steady state' flowering phenology, during the months of January-March.It shows nocturnal flowering and is most likely pollinated by small bats or nocturnal moths. It appears to be self-compatible and has a relatively low natural fruit-set, perhaps due the sparsity of visitors.

Table 5.4.2. Results of experimental hand-pollinations tretaments with Vriesea hydrophora fruit-set, natural fruit-set, and ISI.

POLLINATION	FRUIT-SET
crosses	66.6% (5/10)
selfs	75% (2/6)
natural fruit-set	55% (11/20)
ISI	1.12

Figure 5.4. Vriesea hydrophora: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



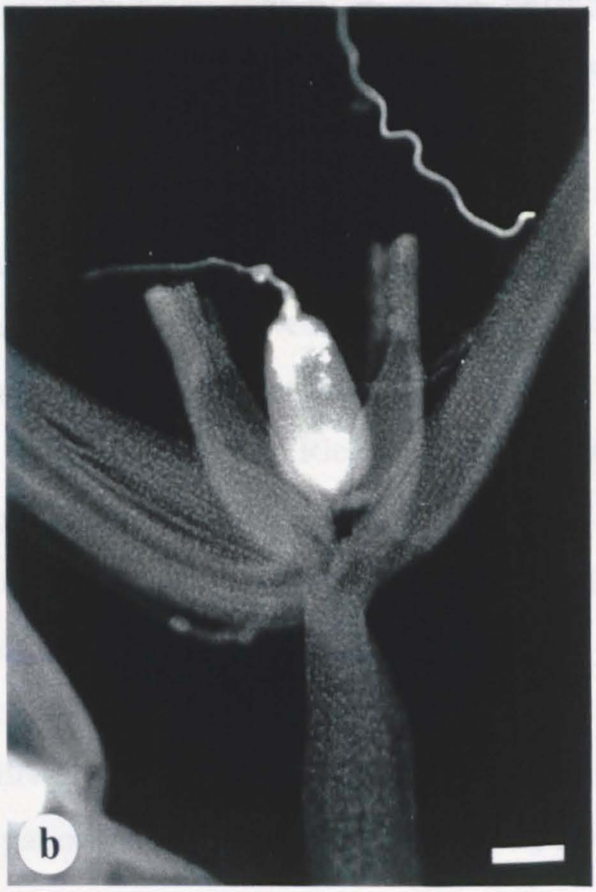
48h- SP: N=3, range 2-21.7%
CP: N=4, range 40.2-65.3%
$P<0.05$

72h- SP: N=6, range 25.1-82.2%
CP: N=4, range 42.5-50.9%
$P>0.05$

96h- SP: N=4, range 71.2-90.9%
CP: N=7, range 41.4-86.3%
$P>0.05$

Plate 5.3. (a) Vriesea hydrophora - branch and flower; (b) penetrated ovule 96 h after self-pollination (scale bars = 100μm).


a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BOTANICAL SPECIMENS: Rio de Janeiro State: Teresópolis, 30/X/1929, Brade 9849 (R); Nova Friburgo, Ecological Reserve of Macaé de Cima, 20/12/1992, G.Martinelli 14729 & D.Miller (RB; cultivated RB, E).

5.5. **Vriesea imperialis Carrière** [Table 5; Figure 5; Plate 5.4,a,b,c; 5.5,a,b,c; 5.6,a,b]

MORPHOLOGY: A large saxicolous plant, with stout, erect stem; Leaves 150cm, numerous, in a funnelform rosette, wholly green or reddish or obscurely maculate toward base. The scape is erect, exceeding the leaves, and the scape bracts are densely imbricate and recurved toward the apex; the inflorescence is composite, slenderly pyramidal. Floral bracts are secund with the flowers, about half as long as the sepals, carinate, and incurved. This species has the largest flowers of the genus, and they are spreading and upwardly secund; pedicels stout, 1cm. Sepals ca. 4cm, reddish; petals over 10cm, white, bearing two large linear appendages at base, flacid and closing the ovary at anthesis. The stigma is convolute-blade.

DISTRIBUTION AND HABITAT: V.imperialis occurs on cliffs and plateaus of high montane grassland, between 1200-2000m altitude, and is endemic of the southeastern sector of the Atlantic Rainforest province. It occurs in large populations in the Serra dos Órgãos, Rio de Janeiro State, and with few populations in Minas Gerais State. The species was studied at two sites: (a) Ecological Reserve of Macaé de Cima, Nova Friburgo, and (b) Pico da Maria Comprida, Araras, Petrópolis.

FLOWERING PHENOLOGY: V.imperialis has a very characteristic phenology with mass flowering periods at intervals of 3-5 years. During a floristic inventory in the area where this species occurs, two populations were observed from 1987 to 1991, and in 1992 during the field research for the present study, and these populations flowered massively in 1988 and 1992, with very few isolated individuals flowering during the years of 1989, 1990 and 1991.

Flowering begins in late November, at the beginning of rainy season, and finishes in early March, with a peak of opened flowers in December and January in both populations. Fruits are mature at the beginning of June (Figure 5). The flowering type was characterized as 'steady state' (Gentry, 1974).

The mean number of flowers which opened per night per plant was 18, (N=6). The mean number of flowers per inflorescence was 505 , and the number of branches in the inflorescence varyed between 36 to 45 branches, with 10 to 18 flowers on each branch (N=4).

POLLINATION BIOLOGY: Vriesea imperialis is a night-blooming species and the flowers, which have a brush-like blossoms, begin to open at c. 18:00h in a relatively brisk manner. When in bud, the closed corolla is cream-yellowish and it changes to white during the anthesis. The petals begin to separate from each other at the base, between 15:30h-16:00h so that eventually they are held together just at the apex (Plate 5.5). At c. 18:00h the petals break free suddenly, exposing the stamens and the style, and continue to reflex-spiral towards the calyx. Whilst the petals are attached at their apex, the stamens and style are held inside the petals, and it is likely that pressure from these causes the petals to separate. As this occurs the stamens and the style are liberated, and the stamens spread around the style in brush-like fashion. Anthers are dorsi-fixed with introrse dehiscence. At this time floral scent is evident (Table 5.5.1).

Anthesis in Vriesea imperialis demonstrated a clear dichogamy between the male and female parts with a marked protandry. In the early hours of the anthesis, the stigma is not receptive and is localized at 1mm above the anthers. Over the next four hours it comes to occupy a position c. 6-7mm above the anthers,

Table 5.5.1. Sequence of anthesis of Vriesea imperialis (N=45)

TIME	COROLLA	STAMENS	STYLE	REWARD
16:00	corolla closed and becoming swollen at base; petals yellow			
17:00	petals held together just at apex, pale yellow			
18:15	petals break free suddenly and becoming spirally recurved toward the calyx; petals white; petal appendage embracing the style	stamens free or bounded by the incurved margins of the petals; anthers begin to release pollen	style free or bounded by the incurved margins of the petals; stigma c. 1mm above the apex of the anthers, closed, dry, and not receptive	nectar
19:10	petals spirally recurved, margins straight; petals white; petal appendages closing the entrance of ovary	stamens free; anthers releasing pollen	stigma c. 2mm above the apex of anthers; closed, dry, and not receptive	nectar
20:30	petal appendages closing the entrance of ovary	anthers releasing pollen	stigma c. 4mm above the apex of anthers; closed, dry, and not receptive	nectar
22:00	petal appendages closing the entrance of ovary	anthers releasing pollen	stigma c. 6mm above the apex of anthers; closed, dry, and not receptive	nectar
23:00	petal appendages with small space between then and the style of 1-2mm	anthers releasing pollen	stigma 7mm above the apex of anthers, opened, wet and becoming receptive	nectar
24:00	petal appendages with small space between then and the style of 1- 2mm	anthers releasing pollen	stigma receptive	nectar
06:00	petals becoming flaccid	anthers empty; filaments becoming flaccid	stigma dry, not receptive	no nectar

Plate 5.4. (a) insects found dead in the rainwater accumulated by the primary bracts due the slippery inflorescence of *Vriesea imperialis*; (b) and (c) *V. imperialis* showing habit and inflorescence.


a
b
c

at which time the stigma becomes wet, open and receptive (see Table 5.5.1). When the buds are young they are joined to the rachis and gradually moving upward and forming a evident space between then, until to reach the completely upward and truly secund position in regard to the rachis and floral bracts.

The colour and the size of the flowers together with the synchronized scent with the opening flowers produced by this species during the anthesis seems to be the most attractive advertisement for the pollinator. The bracts, scape and the branches are dark red with a greasy and slippery surface, probably an adaptation to prevent nectar thieves. Many insects were found dead in the rainwater accumulated by the scape bracts and primary bracts due the slippery parts of inflorescence.

The septal nectaries have three slits in the gynoecial sutures. The petal appendage is acute, 10-12mm long, and embraces the base of the style and partitions off a lower floral chamber, where the nectar is released. During the early stage of anthesis, when the anthers are releasing pollen, the petal appendages completely close off the ovary, with no space evident between them. Subsequently, when the stigma is receptive, each petal appendage makes a short and gradual upward movement, exposing a small gap of 1-2mm between them and the style. It was observed that a light touch on the petal appendage cause a slight movement of the respective pair of stamens in direction of the centre of the flower. Thus mechanical displacement of the petal appendage may help to release pollen onto the body of pollinator, in addition to the other possible functions for these appendages discussed by Harms (1930) McWilliams (1974), and Brown & Terry (1992) viz. protection, prevention nectar loss, delivery, as well as tongue guide.

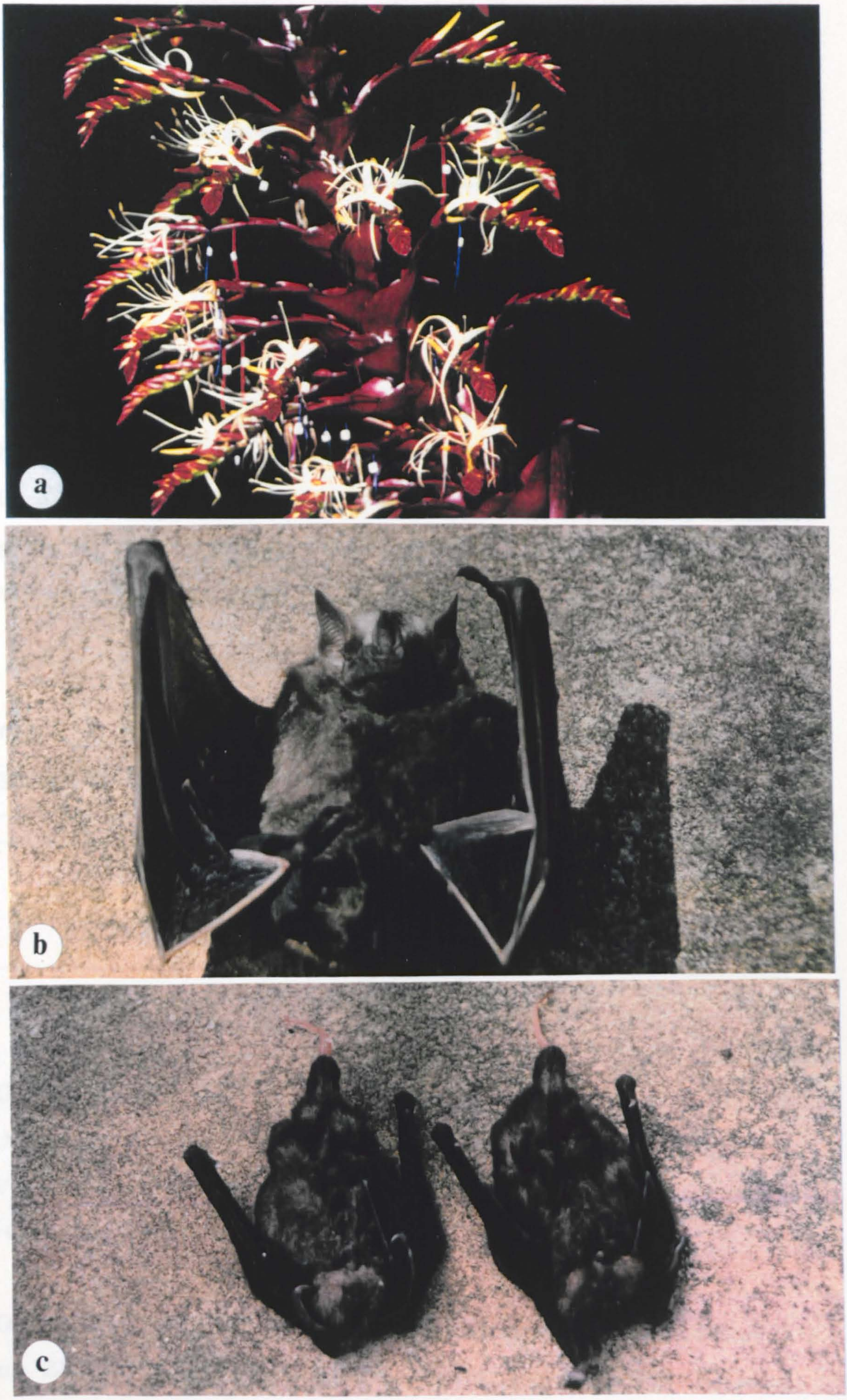
The volume and sugar concentration of nectar (see Table 5) was measured in previously bagged flowers. The production of nectar of Vriesea imperialis is copious, with the mean nectar volume of 168.26μl (N=4, SD±49.9, range 121-228μl) and mean of concentration of sucrose equivalents of 15.6% (N=28, SD±3.62, range 12-23%). Changes in sugar concentration of the nectar were observed between the time intervals of 18:00-22:00h and 22:00-02:00h, with the later period of time presenting higher volume and concentration, which coincides with the time of receptivity of the stigma.

The principal nocturnal visitors observed to visit flowers of Vriesea imperialis were bats, particularly Anoura caudifer, and to a lesser extent Artibeus lituratus. Other night visitors of flowers of Vriesea imperialis included two unidentified hawkmoths (Sphingidae) both of which landed on the base of the stamens and did not contact the anthers or stigma. One individual hawkmoth was observed as a frequent visitor, spending about 20 minutes sucking the excess nectar which rose above the petal appendages, but these appendages seemed form a barrier which prevent proboscises of both hawkmoth species from reaching the nectar in the lower chamber.

Crepuscular and diurnal visitors were the hummingbirds Clytolaema rubricauda, Leucochloris albicollis, Heliotryx aurita and Melanothrochilus fuscus. The species Clytolaema rubricauda seems to be a well-adapted nectar thief, since it visited the flowers of this species at dusk when the petals begin to slacken off exposing the base of filaments and the petal appendages. These birds hovered or landed on the calyx or rachis at this time in an attempt to reach the nectar. In the mornings, this hummingbird also visited some flowers which had opened the previous night. On no occasion were hummingbirds seem to be contact anthers or stigma.

BREEDING SYSTEM: An experimental population was created with a sample of six individuals which were collected in the early stage of flowering from two different natural populations and cultivated in Araras, Petrópolis. Hand-pollinations were performed with previously bagged flowers (N=197) of plants of both populations. Hand-pollinated pistils from different treatments were fixed at 24, 48, 72, 96 and 120 hours after pollination. Fruit-set from hand pollinated flowers, and from tagged flowers left for natural pollination are shown in Table

Plate 5.5. (a) inflorescence of V. imperialis (b) Artibeus lituratus, visitor of flowers of V. imperialis; (c) Anoura caudifer captured when visiting flowers of V. imperialis.


a
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c

5.5.2 Fruit-set from selfed flowers was the same as that for crossed-flowers so V.imperialis is obviously a self-compatible species. However, observations of pollen tube growth and ovule penetration in pistils fixed at 96 and 120 after hand-pollination showed that although self-pollen germinated prolifically on the stigma, these was a marked difference in ovule penetrations, with cross-pollen tubes showing markedly enhanced ovule penetrations at 96 h, and also at 120 h (Figure 5.5.1).

SUMMARY: Vriesea imperialis exhibits 'steady state' (Gentry, 1974) flowering phenology, during the months of November, December, January, February and March. It has nocturnal flowering, and is bat-pollinated, being visited by Anoura caudifer and Artibeus lituratus in the study area. It appears to be self-compatible, and has a high natural fruit-set.

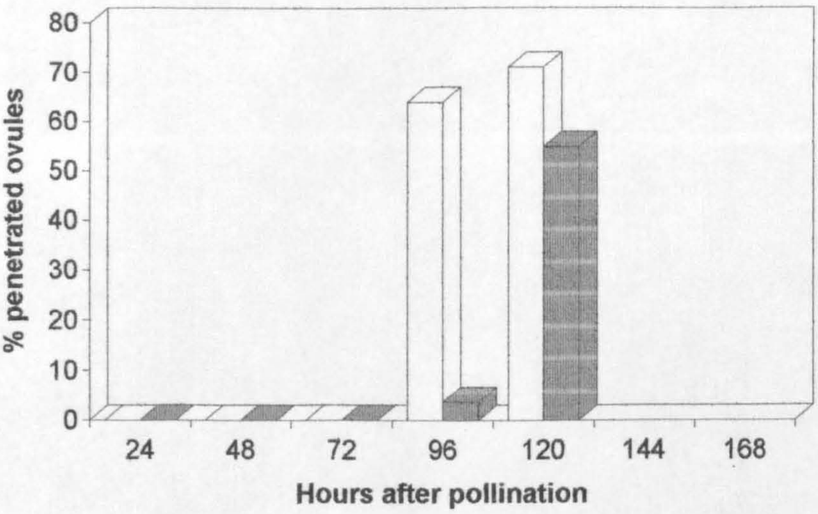
Table 5.5.2. Results of experimental hand-pollinations treatments with Vriesea imperialis fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	84.3% (43/51)
selfs	85.4% (41/48)
natural fruit-set	92% (46/50)
ISI	1.01

BOTANICAL SPECIMENS: Rio de Janeiro State: Petrópolis, 06/III/1984, G.Martinelli 9835 (RB); idem, 28/IV/1977, G.Martinelli 1681 (RB); idem, 20/XII/1992, G.Martinelli 14727 (RB; cultivated RB, E); Nova Friburgo, Macaé de Cima, 12/I/1993, G.Martinelli 14799 (RB).

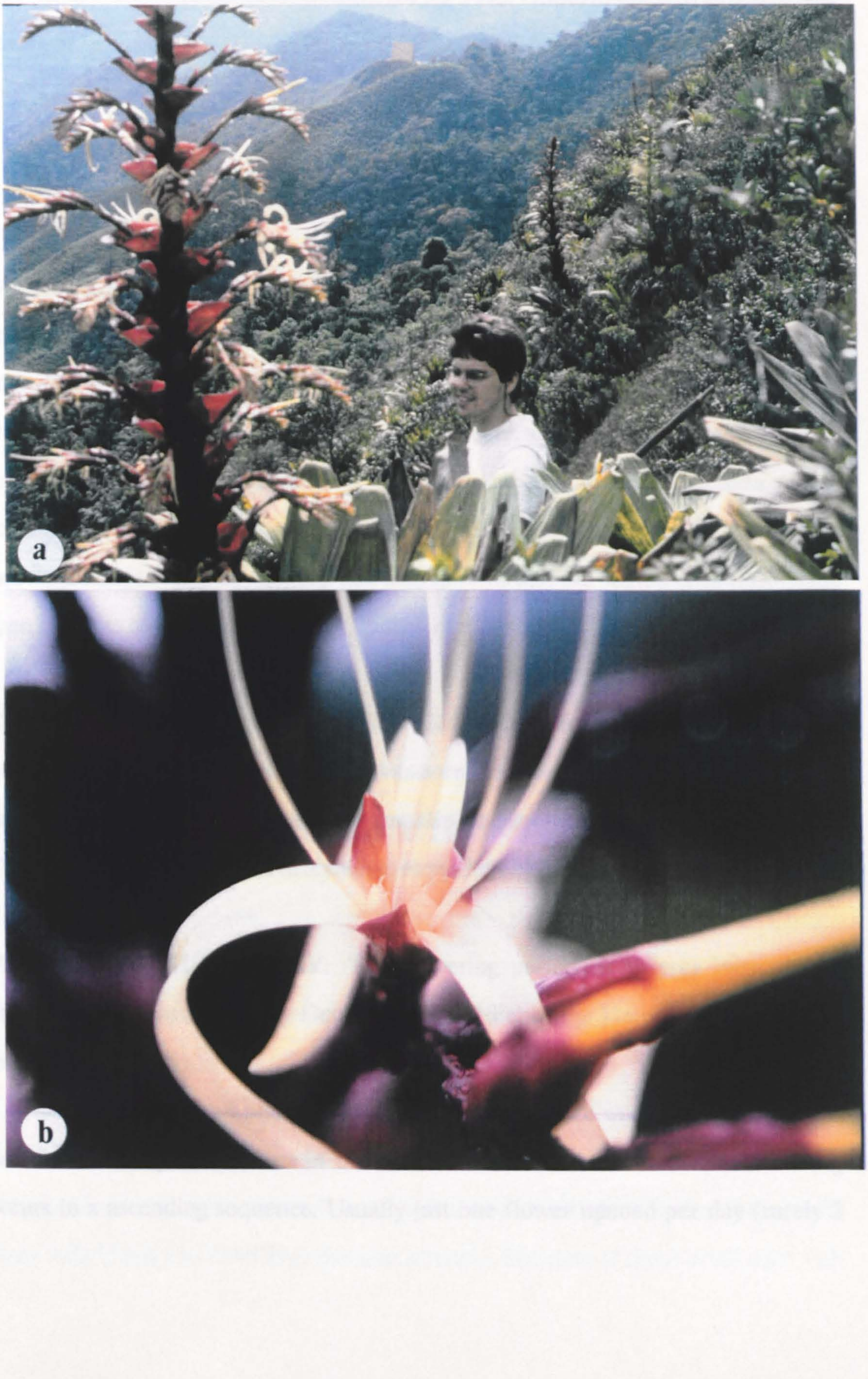
ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Nova Friburgo, Macaé de Cima, 22/XI/1992, G.Martinelli & R.Pineschi 914: Anoura caudifer (R); idem,

Figure 5.5. Vriesea imperialis: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



96h- SP: N=10, range 0-29.3%
CP: N=7, range 52.4-74.9%
120h- SP: N=5, range 38.9-58.2%
CP: N=6, range 59.7-83%
$P<0.05$

Plate 5.6. (a) population of Vriesea imperialis in Macaé de Cima at 1600m; (b) flowers of V. imperialis showing the appendages at base of the petals.


a
b

22/XI/1992, G.Martinelli & R.Pineschi 915: A.caudifer (R); idem, 22/XI/1992, G.Martinelli & R.Pineschi 916: A.caudifer (R); idem, 23/XI/1992, G.Martinelli & R. Pineschi 917: A.caudifer (R); idem, 23/XI/1992, G.Martinelli & R.Pineschi 918: Artibeus lituratus (R).

5.6. Vriesea incurvata Gaudichaud [Table 5; Figure 5; Plate 5.7,b]

MORPHOLOGY: Epiphytic plants, with the leaves green, or sometimes purple toward the apex and forming a spreading rosette. The scape is erect, and shorter than the leaves. Inflorescence simple, many flowered, strongly compressed, with the floral bracts red with yellow margins, imbricate, and always covering the rachis and sepals. Flowers are erect with the petals all issuing from one side of the inflorescence; pedicels stout and short; sepals to 27mm, and petals c. 5cm, bearing two appendages at base; stamens and stigma exserted, the stigma convolute-blade type.

DISTRIBUTION AND HABITAT: This species is found as an epiphyte in the moist forest formations of southeastern sector of the Atlantic Rainforest province, from sea level to 1000m from Rio de Janeiro to Santa Catarina States. This species was studied in Paratymirim at sea level.

FLOWERING PHENOLOGY: The flowering period of Vriesea incurvata in the study area was from early December to mid-February. Mature fruits occurs by mid-May (Figure 5).

The mean number flowers per inflorescence was 14 (N=5), and the first flowers to open are those of the base of the inflorescence such that flowering occurs in a ascending sequence. Usually just one flower opened per day (rarely 2 flowers) with an interval of 2-3 days between each flower. The availability of the flowers was characterized as 'steady state' type (Gentry, 1974).

Vriesea incurvata is diurnal-blooming species and the flowers begin to open around 06:30h, with a duration of c. 13h. The complete sequence of the anthesis is shown in the Table 5.6.1.

POLLINATION BIOLOGY: Anthesis in Vriesea incurvata demonstrated a distinct dichogamy with a marked protandry. In the early hours of the anthesis, the stigma was not receptive and was placed at the same height as the apex of the anthers, but it gradually extended to reach c. 5mm above the anthers some 5 hours later, at which time the stigma become receptive (see Table 5.6.1).

The colour of the floral bracts in this species seems to be the most important advertisement to the pollinator, since some two thirds of the flower are hidden by the bracts and only the apex of the petals is visible. The petals are yellow, and the convolute-blade stigma, the style, and the filaments are white.

The sepal nectaries were not studied in this species but are likely to be the same as in other species of the genus Vriesea. The petal appendages are rounded and contact the style near the base during the anthesis, partitioning the intrafloral chamber in a lower compartment, where the nectar is released.

Nectar in Vriesea incurvata was present as flower opens until around 17:45h. The sugar concentration of nectar (see Table 5) was measured in previously bagged flowers. The maximum volume of nectar measured in a single flower was 32.58μl and the mean concentration of sucrose equivalents was of 22.2% (N=5, SD±1.73, range 19-30%). No changes in sugar concentration were observed during the period of anthesis.

The only visitor observed to visit flowers of Vriesea incurvata was the hummingbird Amazilia fimbriata. This vector did not show very distinct pattern of constancy in its visits, although it seemed to have a definite itinerary through the plant individuals and flowers in the area of study. The time of duration of each visit

Table 5.6.1. Sequence of anthesis of Vriesea incurvata (N = 18)

TIME	COROLLA	STAMENS	STIGMA	REWARD
06:30	corolla opening; petals straight	anthers not releasing pollen	stigma at the height at the apex of the anthers, dry, not receptive	releasing nectar
07:30	corolla open; petals recurved at apex	anthers releasing pollen	stigma 2mm above the apex of the anthers, dry, not receptive	releasing nectar
10:00	corola open	anthers releasing pollen	stigma 4mm above the apex of anthers, becoming wet, not receptive	releasing nectar
11:00	corolla open	anthers releasing pollen	stigma 5mm above the apex of the anthers, wet, receptive	releasing nectar
17:00	corolla beginning to close; petals becoming pale	anthers empty	stigma wet, receptive	releasing nectar
17:40	corolla closed	stamens dry	stigma dry, not receptive	no nectar

to a flower was of c. 1.5 seconds. The hummingbird received loaded pollen in the forehead, touching the stigma when introducing the beak into the flower, and when leaving the flowers.

BREEDING SYSTEM: An experimental population was created with a sample of 5 plants which were collected in the early stage of flowering from two different natural populations and cultivated in Araras. A total of 26 flowers were used in self- and cross- hand-pollinations with previously bagged flowers. A subsample of pistils (selfs and crosses) were fixed at 72h only, and the remaining flowers were left to set fruit (Table 5.6.2). Fruiting success was higher in the crossed flowers, but the ISI indicates tha V.incurvata is a self-compatible species

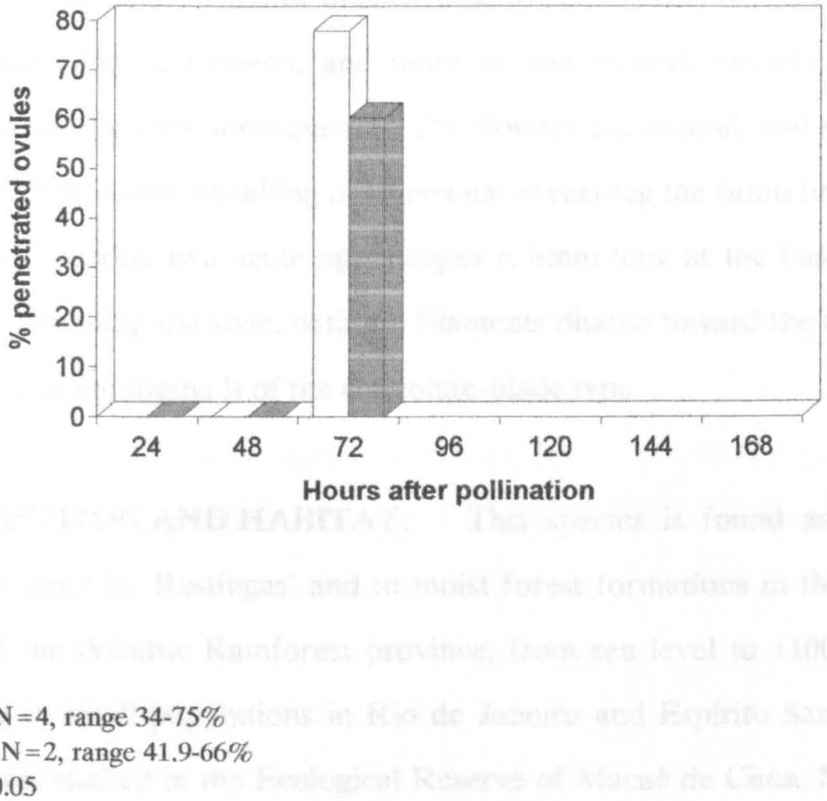
Table 5.6.2. Results of experimental hand-pollinations treatments with Vriesea incurvata fruit-set, natural fruit-set, and ISI.

POLLINATION	FRUIT-SET
crosses	40% (2/5)
selfs	25% (1/4)
natural fruit-set	-
ISI	0.62

For both self- and cross-pollinated pistils the pollen grains germinated prolifically on the stigma and a mass of pollen tubes reached the ovules around 72 hours after pollination (Figure 5.6.1).

SUMMARY: Vriesea incurvata exhibits 'steady state' flowering phenology, during the months of December-February. It has diurnal flowering, and is hummingbird pollinated, being visited exclusively by Amazilia fimbriata in the study area, and it appears to be self-compatible.

Figure 5.6. Vriesea incurvata: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



72h- SP: N=4, range 34-75%
CP: N=2, range 41.9-66%
$P>0.05$

BOTANICAL SPECIMENS: Rio de Janeiro State: Paraty, Fazenda Santa Maria, 14/II/1992, G.Martinelli 14688 (RB; cultivated RB, E).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Paraty, Fazenda Santa Maria, 14/II/1992, G.Martinelli 127-ZOO: Amazilia fimbriata (R).

5.7. Vriesea longiscapa Ule [Table 5; Figure 5; Plate 5.7,a,c]

MORPHOLOGY: Vriesea longiscapa is an epiphytic or terrestrial plant. Leaves are dark green, forming a funnelform rosette. The scape is stout with the scape-bracts erect and foliaceous. The inflorescence is simple, or rarely with 1-3 lateral branches, with the principal or only raceme to 32cm, many flowered; floral bracts are subspreading at anthesis, and more or less secund, initially pale greenish-brown, becoming dark subsequently. The flowers are secund, and spreading, with sepals to 27mm about equalling or somewhat exceeding the floral bracts; the petals are yellow, bearing two acute appendages c. 8mm long at the base; stamens are included, equalling the style, with the filaments dilated toward the apex. The style is curved and the stigma is of the convolute-blade type.

DISTRIBUTION AND HABITAT: This species is found as terrestrial or epiphytic plant in 'Restingas' and in moist forest formations in the southeastern sector of the Atlantic Rainforest province, from sea level to 1100m of altitude, occurring in small populations in Rio de Janeiro and Espírito Santo States. The species was studied in the Ecological Reserve of Macaé de Cima, Nova Friburgo, Rio de Janeiro State, at 1000m of altitude.

FLOWERING PHENOLOGY: The flowering period of Vriesea longiscapa began in late-May and finished in July. Mature fruits were present in early October (Figure 5).

The mean number of flowers per inflorescence was 20 (N=13; range: 14-23), with one or two flowers (rarely 3) opening per night. Flowers at the base of the inflorescence are the first to open such that flowering occurs in a ascending sequence. Vriesea longiscapa is a night-blooming species, and the flowers begin to open at 17:00h. During the first stage of development of the inflorescence, the buds are adpressed to the rachis and change gradually to spreading and secund before anthesis. The floral bracts accompany the flower movements. The availability of the flowers was identified as 'steady state' (Gentry, 1974), and the complete sequence of the anthesis is shown in the Table 5.7.1.

POLLINATION BIOLOGY: Anthesis in Vriesea longiscapa demonstrated a clear dichogamy with a marked protandry. Bract colour in this species is different to that of the majority of day-blooming taxa, in being dark-green, turning black during the anthesis, and then paler subsequently. The bracts are thus not attractive to the pollinators and this accords with the nocturnal vector. The corolla, on the other hand, seems to be an important advertisement to the pollinator, on account of their pallid colour, as is almost certainly the delicate smell which this species presents.

The septal nectaries have three slits located in each gynoecial suture. The petal appendage is acute and very long, c. 8mm, and in contact with the base of the style partitioning off a lower intrafloral chamber, where the nectar is released. During the pollination experiments with the flowers of Vriesea longiscapa, it was observed that a slightly touch of the petal appendage caused a slight movement of the respective pair of stamens in direction of the centre of the flower. As in V. imperialis, therefore, this movement provide a mechanical function for the petal appendage to assist release of pollen onto the body of the pollinator.

The mean concentration of sucrose equivalent was 15.9% (N=23, SD±2.04, Range 8-19%).

Table. 5.7.1. Sequence of the anthesis of Vriesea longiscapa (N=28).

TIME	COROLLA	STAMENS	STYLE	REWARD
16:00	corolla beginning to open; petals pale yellow			
17:00	corolla open; petals yellow	anthers not releasing pollen	stigma at the same height of the middle of the anthers; dry, no receptive	nectar
18:00	corolla open; petals yellow	anthers releasing pollen	style becoming to curve such that the stigma appears to be upward; stigma closed , not receptive	nectar
19:00	corolla open; petals yellow	anthers releasing pollen	style curved, stigma 1-2mm above the apex of the anthers, dry, not receptive	nectar
20:00	corolla open; petals yellow with few brown-reddish marks to the apex	anthers releasing pollen	stigma 3mm above the apex of anthers, becoming wet and receptive	nectar
22:00	corolla open; petals yellow with brown-reddish marks at apex	anthers releasing pollen	stigma receptive, 3mm above the apex of the anthers	nectar
00:00	corolla open; petals yellow with brown-reddish marks in all extension	anthers releasing pollen	stigma receptive, 3mm above the apex of the anthers	nectar
03:00	corolla open; petals becoming brown-reddish	anthers releasing pollen	stigma receptive, 3mm above the apex of anthers	nectar
06:00	corolla closing	stamens dry; anthers empty	stigma dry	no nectar

No pollinators were observed despite several hours of observation in different nights. It is most likely that this species is pollinated by small bat species such Anoura caudifer or Glossophaga soricina, and/or perhaps large nocturnal sphingid moths.

BREEDING SYSTEM: An experimental population of Vriesea longiscapa was created with a sample of 13 individuals which were collected from the natural population and cultivated in Araras. The hand-pollinations (N=88) were performed with these plants, and a subsample of hand-pollinated pistils were fixed at 72h and 96h intervals after pollination. Fruit-set from the remaining hand-pollinated flowers was followed until maturation, and an estimate of natural fruit-set was obtained from tagged flowers on different plants in the natural population. It is of interest to note that despite the lack of visitors during the observation periods, the natural fruit-set is this species is high (Table 5.7.2).

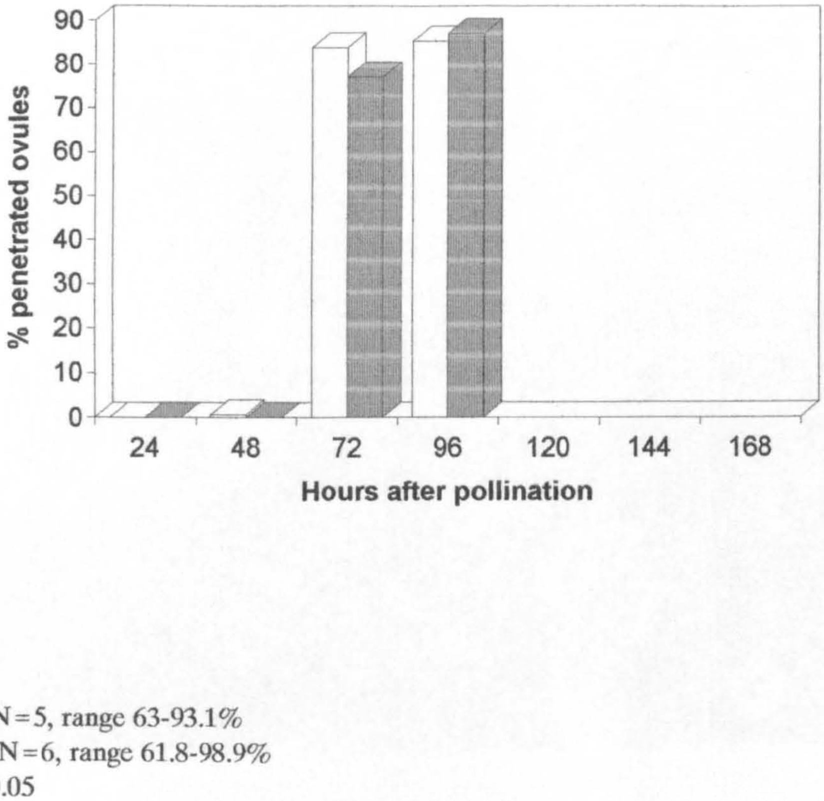
In both self- and cross- hand-pollinations the pollen grains germinated prolifically on the stigma and grow at equal rates down the style. By 48 hours both types of pollen tubes had reached the ovary and at

this time some initial ovule penetrations were observed in selfed pistil. By 72 hours post-pollination virtually all ovules have been penetrated in both selfed and crossed pistils. (Figure 5.7.1).

Table 5.7.2. Results of experimental hand-pollinations treatments with Vriesea longiscapa fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	60% (6/10)
selfs	25% (3/12)
natural fruit-set	86% (43/50)
ISI	0.41

Figure 5.7. Vriesea longiscapa: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



72h- SP: N=5, range 63-93.1%
CP: N=6, range 61.8-98.9%
P>0.05
96h- SP: N=4, range 85-89.4%
CP: N=6, range 72.9-98.9%
P>0.05

Plate 5.7. (a) *Vriesea longiscapa* flowers; (b) penetrated ovules of *Vriesea incurvata*, at 72 h after self-pollination (scale bars = 100μm); (c) *V. longiscapa* inflorescence.

DISTRIBUTION AND HABITAT: This species is found as a saxicolous or terrestrial plant, from near sea level to 400m in 'Restingas' and maritime granitic outcrops, extending from Rio de Janeiro to Paraná and Santa Catarina States. The species was studied at Paranaguá at sea level.

SUMMARY: Vriesea longiscapa exhibits 'steady state' flowering phenology (Gentry, 1974), during the months of May-July. It has a nocturnal flowering, and is most likely to be pollinated by small bats or nocturnal moths. It appears to be self-compatible, and has a high natural fruit-set.

BOTANICAL SPECIMENS: Rio de Janeiro State: Sta. Maria Madalena, 24/III/1955, E.Pereira 1320 (RB); Nova Friburgo, Morro da Caledônia, 09/V/1978, G.Martinelli 4434 (RB); Ecological Reserve of Macaé de Cima, 26/VII/1992, G.Martinelli 14694 (RB; cultivated RB, E); Macaé, Pico do Frade de Macaé, 16/IV/1982, G.Martinelli 8731 (RB).

5.8. Vriesea neoglutinosa Mez [Table 5; Figure 5; Plate 5.8,a,b]

MORPHOLOGY: Plant usually saxicolous, 1-2m high, growing in exposed rocky localities. The leaves are numerous forming a funnelform rosette. Inflorescence with with an erect scape with scape red bracts, paniculate, lustrous, the racemes 6-15 flowered; floral bracts imbricate before anthesis, then divergent and enfolding the sepals, coriaceous, yellow-greennish or reddish. Flowers with pedicels c. 7mm, sepals elliptic, c. 29 mm; petals 6-12 mm longer than the sepals, ligulate, bearing two acute appendages at base; stamens and style exserted, stigma convolute-blade type.

DISTRIBUTION AND HABITAT: This species is found as a saxicolous or terrestrial plant, from near sea level to 400m in 'Restingas' and maritime granitic outcrops, extending from Rio de Janeiro to Paraná and Santa Catarina States. The species was studied at Paratymirim at sea level.

FLOWERING PHENOLOGY: The flowering period of Vriesea neoglutinosa in the area studied, extended from January to the end of March (Figure 5), with a peak of flowering was observed in mid-February. The flowers of the base of the branches are the first to open, with normally one flower per day in a single scaped individual, but sometimes around 2-3 flowers (with a single flowers on each branch of the inflorescence) on the same plant, and then gradually opening the adjacent superior one in a ascending sequence. The availability of the flowers was identified as 'steady state' (Gentry, 1974). The mean number of flowers per inflorescence was 84 (N = 12), with some individuals presenting up to 130 flowers.

Fruits were mature at the end of May, at which time, the floral bracts and the sepals were still attached to the fruit and no fruit predation was observed during the fruit development.

Vriesea neoglutinosa is a day-blooming species and the flowers begin the anthesis around 06:00h and finishing c. 13 hours latter. The complete sequence of anthesis is showed in the Table 5.8.1.

POLLINATION BIOLOGY: Flowers of Vriesea neoglutinosa are dichogamous with marked protandry. In the early hours of the anthesis the stigma is not receptive and occurs at the same height as the anthers, but style elongation over a period of c. 5 h exserts the stigma to c. 10mm above the top of the anthers, at which time the stigma is receptive (see Table 5.8.1).

The colour of the bracts and branches together with the colour of the corolla of V.neoglutinosa seems to be the most important advertisements to the pollinator (Plate 5.8). The lower half of the flower of this species is hidden by the floral bracts, and the stigma is yellow with the same colour of the petals. When the inflorescence is young, the buds and the floral bracts, which are appressed to the rhachis, present a marked viscous exudation, which begins to diminish during the fruiting.

Table 5.8.1. Sequence of the anthesis of Vriesea neoglutinosa (N = 17).

TIME	COROLLA	ANTHERS	STIGMA	REWARD
06:00	corolla opening and becoming secund	anthers at the same height of the petals; not releasing pollen	stigma 2-3mm below the base of the anthers; dry, not receptive	nectar
07:00	corolla open; apex of the petals recurved	anthers 2mm above the petals; anthers releasing pollen	stigma at the same height of the base of the anthers, dry, not receptive	nectar
08:00	corolla open	anthers 4mm above the petals; releasing pollen	stigma at the middle of the height of the anthers, dry, not receptive	nectar
09:00	corolla open	anthers 5mm above the petals; releasing pollen	stigma at the same height of the apex of the anther dry, not receptive	nectar
10:00	corola open	anthers releasing pollen	stigma 2-3mm above the apex of the anthers, dry, not receptive	nectar
11:00	corolla open	anthers releasing pollen	stigma 5mm above the apex of anthers, becoming wet and receptive	nectar
12:00	corolla open	anthers releasing pollen	stigma 8mm above the apex of the anthers, wet, receptive	nectar
13:00	corolla open	anthers releasing pollen	stigma 10mm above the apex of anthers, wet, receptive	nectar
17:00	corolla open	anthers empty	stigma becoming dry	nectar
19:00	corola becoming to close	filaments becoming dry	stigma dry, not receptive	no nectar

The septal nectaries have three slits near the base of each gynoecial suture. The petal appendage is acute and during the anthesis it embraces the base of the style, partitioning the intrafloral chamber in a lower chamber, where the nectar is collected.

The nectar of V.neoglutinosa was available from the time the flowers open until c. 19:00h. The production of nectar of Vriesea neoglutinosa was copious relative to the size of the flowers, with mean volume of 63.3μl (N=6, SD±16.8, range 54.9-85.3μl). No significant differences in nectar volume was observed at two different time intervals (07:00-10:00h and 10:00-13:00h). The mean of concentration of sucrose equivalents was 19.8% (N=27, SD±2.9, range 16-28%). The sugar concentration showed high percentage of sucrose equivalents at the later interval (mean of 18.8% at 07:00-10:00h and 22% at 10:00-13:00h), which coincided with the phase of receptivity of the stigma (see Table 5.8.1).

The visitors to flowers of Vriesea neoglutinosa at the study site were the hummingbirds Amazilia fimbriata and Chlorostilbon aureoventris. This species seems to be pollinated exclusively by hummingbirds since no other visitors were observed at the flowers. The most effective pollinator was Amazilia fimbriata due to its frequency and behaviour at the flowers. The routine visiting behaviour of this hummingbird was as follows. Individuals of Vriesea neoglutinosa with 2 or 3 open flowers in the inflorescence were visited by Amazilia fimbriata. All flowers were visited before the hummingbird moved on to next plant. This hummingbird received pollen in the forehead, sides of the neck and on the infra-ocular region, touching the stigma at each visit, when hovering in the flowers. This species showed a very strong pattern of constancy in its visits to V.neoglutinosa flowers and the individuals visited, and repeated the same itinerary of visits from flower to flower and from plant to plant, with intervals that varied between 11-40 minutes.

BREEDING SYSTEM: An experimental population was created consisting of nine individuals which were collected from two different natural populations. The

Plate 5.8. (a) the hummingbird Chlorostilbon aureoventris visiting flower of Vriesea neoglutinosa; (b) inflorescence of V. neoglutinosa.


a


b

hand-pollinations were performed in previously bagged flowers with this artificial population (N=136). Fruit-set from hand-pollinations and from sample flowers tagged for natural fruit-set (N=60) are shown in Table 5.8.2.

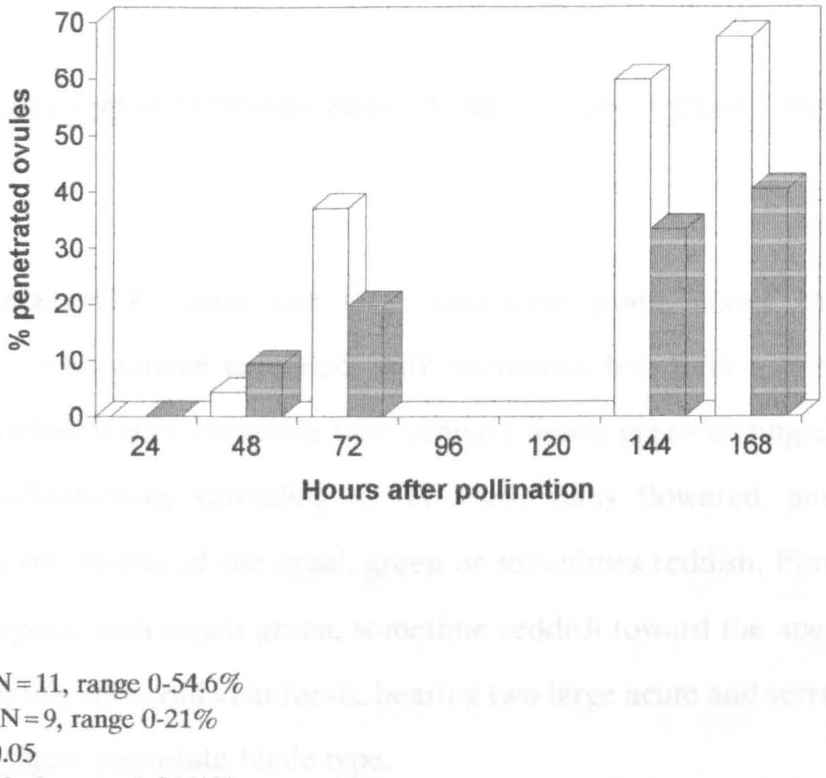
In both self- and cross-pollinated pistils the pollen grains germinated prolifically on the stigma and a mass of pollen tubes could be distinguished in the style. In all styles sampled at 24 hours (N=5), cross-pollen tubes had extended further than selfs (cross-pollen tubes had a mean length of 25mm vs. 18mm in selfs), but curiously in the samples of pistils at 48 hours, ovule penetration by self-pollen tubes exceeded those in crosses. At all other sampled intervals (no crossed pistils were available for 96 and 120 hours) ovule penetration in crossed pistils considerably exceeded those in selfed ones (Figure 5.8.1). However, very little difference was found in fruit-set between selfs and crosses, and the ISI value of 0.84 indicates a self-compatible species (Table 5.8.2).

Table 5.8.2. Results of experimental hand-pollinations treatments with Vriesea neoglutinosa fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	36.8% (7/19)
selfs	31% (9/29)
natural fruit-set	82% (41/50)
ISI	0.84

SUMMARY: Vriesea neoglutinosa exhibits 'steady state' flowering phenology during the months of November to March. It has a diurnal flowering, and is hummingbird-pollinated, being visited by Amazilia fimbriata and Chlorostilbon aureoventris. It appears to be self-compatible and has a high natural fruit-set.

Figure 5.8. Vriesea neoglutinosa: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



48h- SP: N=11, range 0-54.6%
CP: N=9, range 0-21%
P>0.05
72h- SP: N=2, range 0-54%%
CP: N=16, range 0-91%%
P<0.05
144h- SP: N=5, range 9.2-55.7%
CP: N=4, range 54.1-71.5%
P<0.05
168h- SP: N=2, range 37.2-48.2%
CP: N=9, range 44.7-85%
P>0.05

BOTANICAL SPECIMENS: Rio de Janeiro State: Casemiro de Abreu, Barra de Sâo João, 20/III/1979, G.Martinelli 5697 (RB); Macaé, 30/IX/1974, G.Martinelli 493 (RB; GUA); Saquarema, Massambaba, 15/VIII/1986, G.Martinelli 11683 & al. (RB); Paraty, Paratymirim, 12/II/1992, G.Martinelli 14687 & P.Gibbs (RB; cultivated RB, E).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 17/12/1992, G.Martinelli 119-ZOO: Amazilia fimbriata (R).

5.9. **Vriesea regina (Vellozo) Beer** [Table 5; Figure 5; Plate 5.9a,b,c,d; 5.10,a,b,c; 5.11,a,b,c]

MORPHOLOGY: Stout and large saxicolous plant, about 2m high with an extended inflorescence extended, with numerous leaves in a dense funnelform rosette. Inflorescence bipinnate with primary bracts green or tinged red; branches of the inflorescence spreading to recurved, many flowered, and floral bracts equalling the middle of the sepal, green or sometimes reddish. Flowers distichous and divergent, with sepals green, sometime reddish toward the apex; petals 10cm, white, spirally recurved at anthesis, bearing two large acute and serrate appendages at base; stigma convolute-blade type.

DISTRIBUTION AND HABITAT: This endemic species is found as a striking, large, saxicolous plant on sloping granitic outcrops from near the sea level to 500m of altitude, in the southeastern sector of the Atlantic Rainforest province. It occurs in large populations in the Rio de Janeiro State. The species was studied in Paraty, Paratymirim, at sea level.

FLOWERING PHENOLOGY: The endemic Vriesea regina has a very characteristic phenology with pulsed flowering episodes at intervals of 2-3 years. The flowering period extended from December until February, with a flowering peak around January. Mature fruits were present between April-May (Figure 5).

The mean number of flowers per inflorescence was 86 (N=8), with some individuals presenting up to 122 flowers. Flowers at the base of the inferior branches of the inflorescence are the first to open such that flowering occurs in a ascending sequence. This species open 2 to 5 flowers per day which last until the sunrise and the availability of the flowers was characterized as 'steady state' (Gentry, 1974).

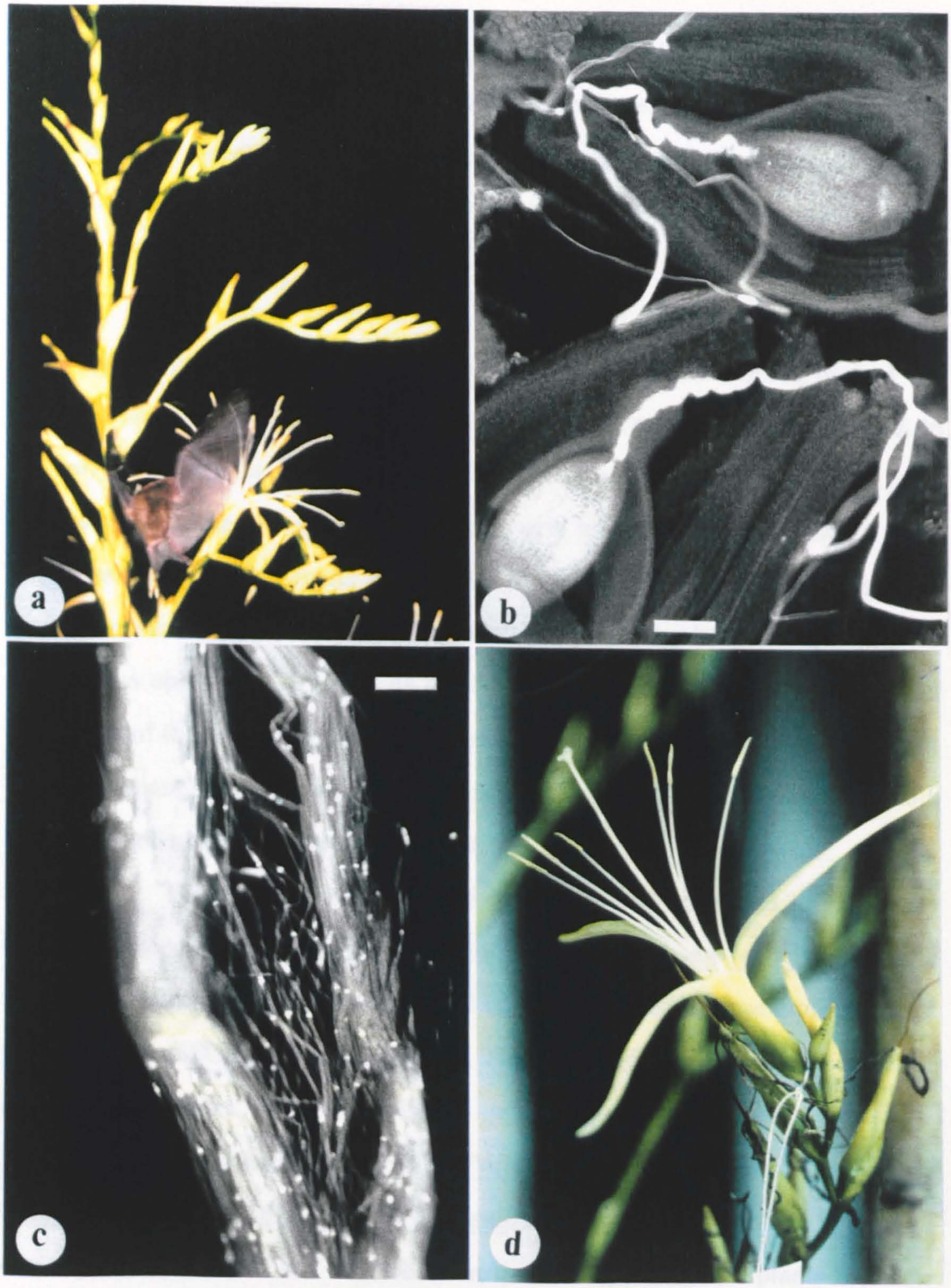
POLLINATION BIOLOGY: Vriesea regina is a night-blooming species and the flowers begin to open relatively rapidly at c. 18:00h. The sequence of flower opening is remarkably similar to that of V. imperialis - when in bud, the closed corolla is yellowish and it changes to white during the anthesis. The petals begin to separate from each other at the base, between 16:00-17:00h, so that eventually they are held together just at the apex. At c. 18:00h the petals break free suddenly, exposing the stamens and the style, and continue to reflex-spiral towards the calyx. Whilst the petals are attached at their apex, the stamens and style are held inside the petals after the corolla has opened. When the petals finally separate and begin to unroll, the stamens and the style are liberated. The stamens become spread around the style in a brush-like fashion. The complete sequence of the anthesis are showed in the Table 5.9.1.

Anthesis in Vriesea regina demonstrated a distinct dichogamy with a marked protandry. In the early hours of the anthesis, the stigma is not receptive and is localized at the same height of the apex of the anthers, gradually extending to reach c. 4mm above the apex of the anthers some 3 hours later, at which time the stigma was receptive (see Table 5.9.1).

Table 5.9.1. Sequence of the anthesis of Vriesea regina (N = 15)

TIME	COROLLA	STAMENS	STYLE	NECTAR
16:00	beginning to separate from each other at the base; petals pale yellow			
17:00	petals held together just at apex, changing to white			beginning to release nectar
18:30	petals detached and break free suddenly, exposing the stamens and style, white	anthers not releasing pollen; stamens spreading	stigma at the same height of the apex of the anthers, dry, not receptive	nectar
20:00	petals recurved spirally, scent evident	anthers releasing pollen	stigma 2mm above the apex of the anthers; becoming wet and receptive	nectar
22:00	scent evident	anthers releasing pollen	stigma 3mm above the apex of the anthers, wet, receptive	nectar copious
02:00	petals scentless	anthers almost empty	stigma 4mm above the apex of the anthers, receptive	nectar copious
04:30	corolla becoming flaccid	stamens flacid	stigma becoming dry, not receptive	no nectar

Plate 5.9. (a) the bat Glossophaga soricina visiting Vriesea regina flower; (b) V. regina penetrated ovules at 96 h after self-pollination (scale bars = 100μm); (c) V. regina - pollen tubes at the end of the style in self-pollinated pistil at 96 h after pollination (scale bars = 100μm); (d) V. regina - flower.


a
b
c
d

The pallid white colour and the size of the flowers, together with the synchronized liberation of scent as the flowers open seem to be the most attractive advertisement for the pollinator. The bracts, scape and the branches of the inflorescence are green or sometimes green-reddish, with a greasy and slippery surface.

The septal nectaries have three slits in the gynoecial sutures. The petal appendages are large, acute and serrate, and they embrace the base of the style and thus cut off a lower intrafloral chamber where the nectar is released. In the early stages of the anthesis, when the anthers are releasing pollen, the petal appendages completely close off the ovary, with no space evident between then. Subsequently, when the stigma is receptive, the petal appendage make a short and gradual movement upward, exposing a small gap of 1-2mm between then and the style. It was observed that a slightly touch on the petal appendage caused a slight movement of the respective pair of stamens in direction of the centre of the flower. This movement may be a mechanical function for the petal appendage to help deposit of pollen on the body of pollinator.

The sugar concentration of the nectar was measured in previously bagged flowers. The maximum volume of nectar of Vriesea regina in a single flower was 218μl at 19:40h, and mean of concentration of sucrose equivalents of 12.4% (N=21, SD±3.86, range 8-19.9%). The nectar of this species was available as the flowers opens.

The principal visitors of Vriesea regina were the bats Anoura caudifer, Anoura geoffroy, Artibeus lituratus and Glossophaga soricina. With all of these species of bats it was observed that the bats approach the plants from the same general direction, with the bouts of activity occurring at intervals of 15 to 50 minutes, and the time of a visit to each flower was less than one second. The individuals of A. caudifer and A. geoffroy captured in the mist-net had pollen grains of V. regina on the snout, sides of the face, and inner surface of the wing (Plate 5.9).

Other night visitors of flowers of this species, included a nocturnal hawkmoth (Sphingidae), which visited the flowers alone or in pairs. (Plate 5.9).

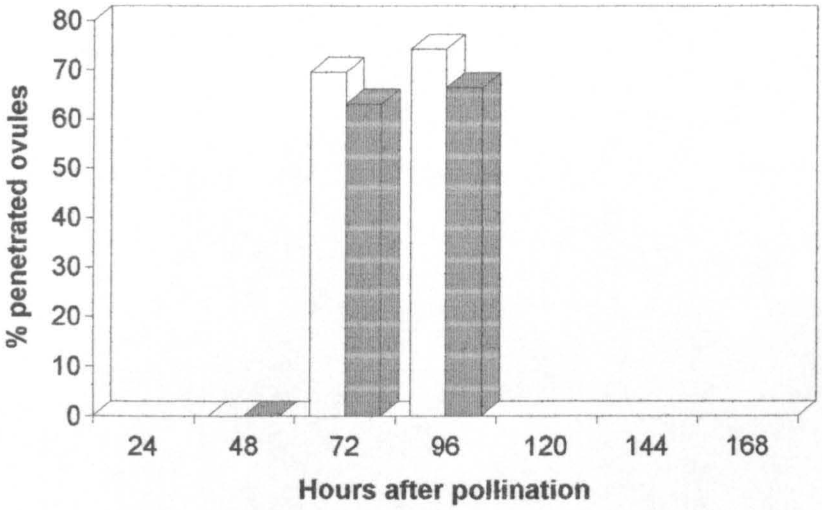
Crepuscular and diurnal visitors were the hummingbirds, *Melanotrochilus fuscus* and *Amazilia fimbriata*, both acting as opportunistic nectar thieves, since they visited the flowers at dusk when the petals began to slacken off, exposing the base of the filaments. These birds hovering or landing on the calyx or rhachis at this time attempted to reach the nectar. In the mornings, these hummingbirds also visited flowers which had opened the previous night. On no ocasion were hummingbirds seen to contact the anthers or stigma.

BREEDING SYSTEM: An experimental population was created with a sample of five individuals which were collected in an early stage of flowering from a population at Paraty, and cultivated in Araras. Hand-pollinations were performed in previously bagged flowers (N=74). A subsample of hand-pollinated pistils from different treatments were fixed at 72 h and 96 h after pollination. Fruit-set from the remaining hand-pollinated flowers was followed until maturation, and an estimate of natural fruit-set was obtained from tagged flowers on different plants in the natural population (Table 5.9.2).

This species seems to be self-compatible. In both self- and cross-pollinations the pollen grain germinated prolifically on the stigma and a mass of pollen tubes could be distinguished in the style. By 72 hours both types of pollen tubes had reached the ovary and the penetration of the ovules begin between 48-72 hours with little difference between the incidence of ovule penetration in crossed and selfed pistils (Figure 5.9).

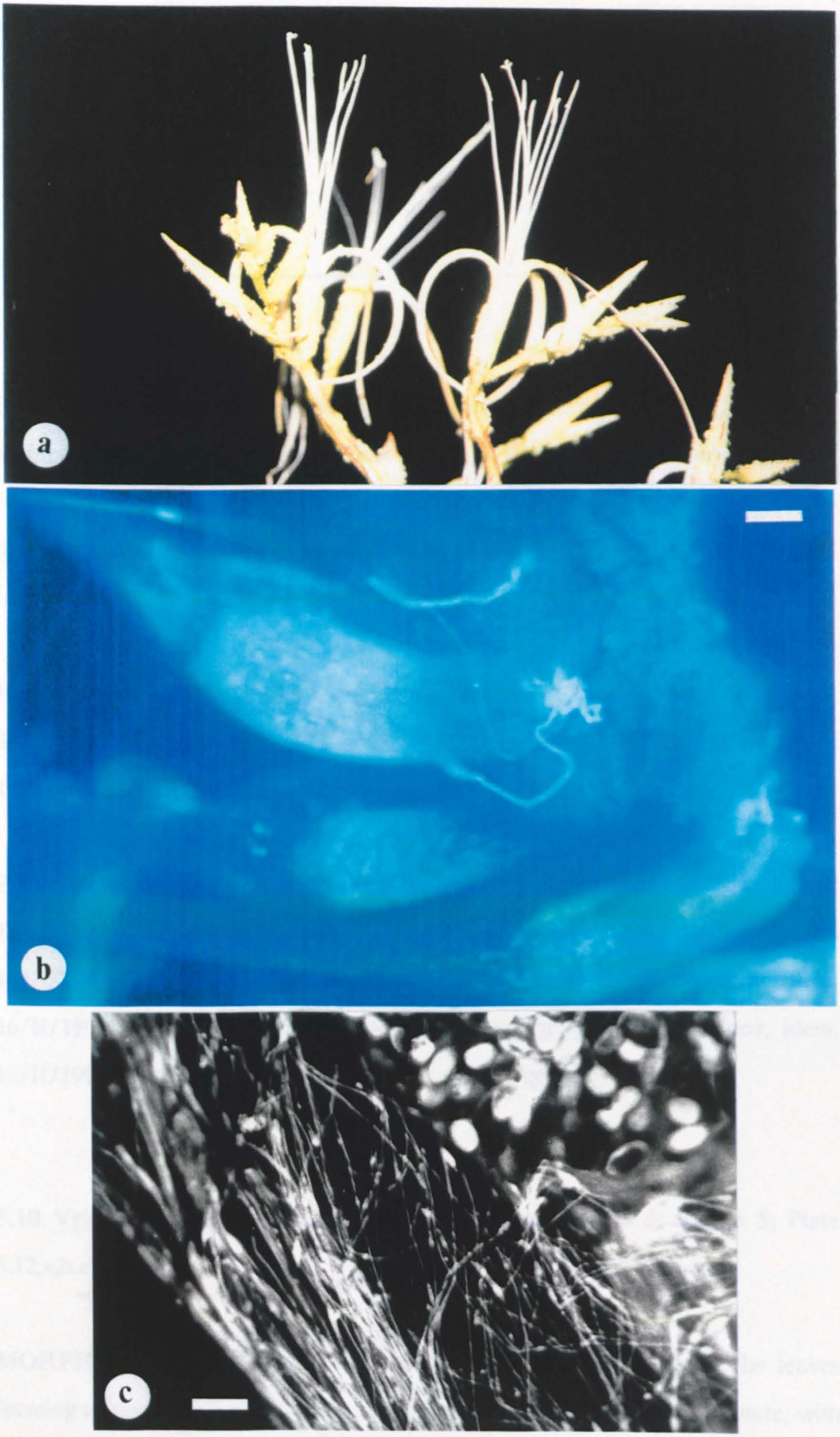
The fruit-set percentage from hand-pollination treatments of transplanted population for which mature fruits were collected and the natural fruit-set are showed in the Table 5.9.2.

Figure 5.9. Vriesea regina: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



72h- SP: mean=53.4% (N=1)
CP: mean=68% (N=2, range 63-73%)
96h- SP: mean=66.5% (N=7, range 60.2-74.7%
CP: mean=74.3% (N=2, range 72.1-76.5%)
$P>0.05$

Plate 5.10. (a) nocturnal flowers of Vriesea regina; (b) V. regina- penetrated ovules at 72 h after self-pollination (scale bars = 100μm); (c) V. regina - mass of pollen tubes of self-pollen grains below the stigma at 96 h after self-pollination (scale bars = 100μm).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b
c

Table 5.9.2. Results of experimental hand-pollinations treatments with Vriesea regina fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	80% (16/20)
selfs	75% (12/16)
natural fruit-set	73.3% (22/30)
ISI	0.93

SUMMARY:Vriesea regina exhibits 'steady state' flowering phenology, during the months of December-February. It has nocturnal flowering, and is bat-pollinated, being visited principally by Anoura caudifer, Anoura geoffroy, and Artibeus lituratus, in the study area. It appears to be self-compatible, and has a high natural fruit-set.

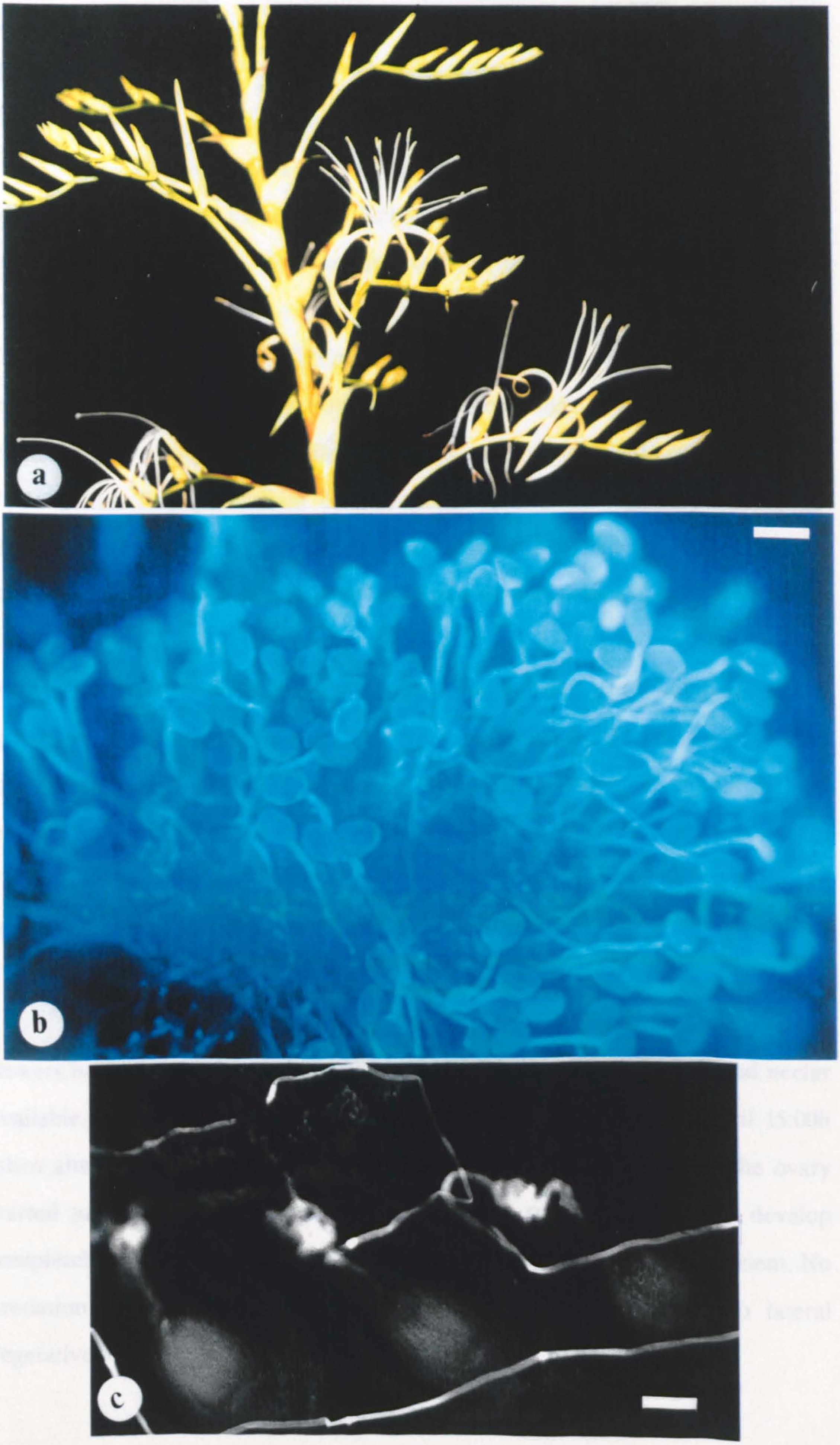
BOTANICAL SPECIMENS: Rio de Janeiro State: Pedra de Itaúna, 08/I/1978, P.Carauta 2810 (RB); Paraty, Paratyimirim, 13/II/1992, G.Martinelli 14691 & P.Gibbs (RB; cultivated RB, E).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 16/II/1992, G.Martinelli & R.Pineschi 919: Artibeus lituratus (RioZoo); idem, 16/II/1992, G.Martinelli & R.Pineschi 920: Anoura caudifer (RioZoo); idem, 16/II/1992, G.Martinelli & R.Pineschi 921: Anoura caudifer (RioZoo); idem, 16/II/1992, G.Martinelli & R.Pineschi 922: Anoura geoffroy (RioZoo).

5.10. Vriesea sparsiflora L.B.Smith var. sparsiflora [Table 5; Figure 5; Plate 5.12,a,b,c]

MORPHOLOGY: Epiphytic or occasionally terrestrial plants, with the leaves forming a funnelform rosette. The inflorescence up to 60cm, laxly bipinnate, with

Plate 5.11. (a) flowers of *Vriesea regina*; (b) self-pollen grains germination at 72 h after pollination in *Vriesea regina* (scale bars = 100μm); (c) *V. regina* - penetrated ovules at 96 h after self-pollination (scale bars = 100μm).


a
b
c

60-130 flowers, with flexuous branches to 30cm long, and 2-7 flowered with the terminal flowers always abortive. The floral bracts are secund with the flower during the anthesis, red, carinate, and turning black at maturity.

The flowers are spreading at anthesis; sepals carinate, 15mm; petals ligulate forming a tubular corolla, 32mm, whitish, and bearing two acute petal appendages at base. The anthers are exserted by 2-4mm from the petals at anthesis.

DISTRIBUTION AND HABITAT: This species is usually epiphytic, and endemic in the wet montane forest of the southeastern sector of the Atlantic rainforest province, between 1000-1300m of altitude, in the Rio de Janeiro and São Paulo States. Two populations of this species were studied at two sites in the Ecological Reserve of Macaé de Cima, at 1200m, Nova Friburgo, Rio de Janeiro State.

FLOWERING PHENOLOGY: The two populations of Vriesea sparsiflora var. sparsiflora which were monitored, flowered synchronously. The flowering period started in mid-September, with the last flowers in late December. A well defined peak of flowering was observed in November. The fruits were mature in late February (Figure 5). Each individual opened 1-4 flowers per day over a period of several months, so that flowering conforms to the Gentry (1974) 'steady state' type. The average of flowers per inflorescence was 68.2 flowers (N = 10, range 40-101).

Vriesea sparsiflora var. sparsiflora is a day-blooming species and the flowers begin to open around 06:00h and were fully open, with pollen and nectar available, one hour later. The anthers released pollen from 07:00h until 15:00h when almost no pollen was found (Table 5.10.1). With fruit initiation the ovary started to swell slowly, and the fruit takes two or three months to develop completely. The calyx remains attached to the fruit throughout development. No predation was observed in sampled fruits. This species produce two lateral vegetative off-shoots during the fruiting time.

POLLINATION BIOLOGY: Vriesea sparsiflora var. sparsiflora flowers are dichogamous with marked protandry. As the flower opens, the convolute-blade stigma type is still closed, and is not receptive, and is located at the same height as the base of the anthers. The style elongated progressively so that by c. 11:00h the stigma projected some 6mm beyond the apex of the anthers, by which time it had unfolded and had a wet appearance, and was receptive (see Table 5.10.1).

The inflorescence of V.sparsiflora var. sparsiflora seems to be the most important attractive feature to the pollinators, with it's bright red coloured branches and bracts. The floral bracts are red, turning pale and black during the anthesis, the calyx is pale-yellow, with the corolla whitish, such that there is a strong colour contrast between the bracts and branches of the inflorescence and the calyx and corolla.

The septal nectaries are inferior, with three outlets in form of slits at the level of the base of the style. The petal appendages during the anthesis, embrace the base of the style, partitioning off a lower intrafloral chamber, where the nectar is collected.

The nectar was present as the flower opened at 06:00h, and continued to be available until 16:00h. Volume and sugar concentration of nectar (Table 5) were measured at different time of the day in previously bagged flowers. The mean volume of nectar was 19.6μl (N = 11, SD ± 7.4, range 12.9-22.7μl), and the mean of sugar concentration was 22.7% (N=25, SD±3.09, range 17-26%). No significant variation in sugar concentration (sucrose equivalents) was observed during the anthesis, but the mean of volume over the time interval of 06:00-13:00h (morning period) was 10.13μl (N=3), whereasbetween 13:00-17:00h, (afternoon period), the volume of nectar was significantly higher, with 18.3μl (N=8) in this latter period.

Table 5.10.1. Sequence of anthesis of Vriesea sparsiflora var. sparsiflora (N=38).

TIME	COROLLA	ANTHERS	STIGMA	REWARD
05:30	closed	apex of anthers touching the apex of the petals	stigma closed, dry, 4mm below the base of anthers	-
06:00	corolla opens; petals white	apex of the anthers at same height of the petals; not releasing pollen	stigma closed , dry, 2mm below the base of anthers; not receptive	nectar
07:00	corolla fully opened; petals white, slightly recurved at apex	apex of anthers 2mm above the apex of the petals; releasing pollen	stigma closed and dry, at same height as the base of anthers; not receptive	nectar
08:00	petals white	apex of the anthers 4mm above the apex of petals; releasing pollen	stigma closed and dry, at same height as the middle of anthers; not receptive	nectar
09:00	petals white	anthers releasing pollen	stigma closed and dry, 1mm above the apex of anthers; not receptive	nectar
10:00	petals white	anthers releasing pollen	stigma beginning to open, wet, 3mm above the apex of anthers	nectar
11:00	petals white	anthers releasing pollen	stigma opened, wet, 5-6mm above the apex of anthers; receptive	nectar
14:00	petals white	anthers almost empty	stigma 6mm above the apex of anthers; receptive	nectar
17:00	petals cream, becoming flaccid	anthers empty	stigma becoming dry	no nectar
18:00	petals yellow, flaccid	stamens flaccid	stigma dry	no nectar

Visitors to flowers of Vriesea sparsiflora var sparsiflora were the hummingbirds Clytolaema rubricauda, Leucochloris albicollis, Stephanoxis lalandi and Phaetornis eurynome. This species seems to be pollinated exclusively by hummingbirds since no other visitors were observed at the flowers. The most effective pollinator was Phaetornis eurynome, which was also the most frequent visitor, since its tongue and beak length are almost the same as that of the corolla of V.sparsiflora var. sparsiflora (c. 33mm). The visiting behaviour of Phaetornis eurynome was almost identical in all visits which were made during 16 hours of observation, on different days and times of the day, for the eight individuals monitored. The duration of each visit to a single flower was around 2 seconds, and the same flower were visited perhaps 11-14 times per day. In all visits the hummingbird touched the stigma of V.sparsiflora. One individual male of Phaetornis eurynome was captured, and a large amount of pollen of V.sparsiflora var. sparsiflora was observed around the beak, on the neck, and, principally, on the forehead. This species of hummingbird showed a strong pattern of constancy, with the same traplining itinerary triplinning in its visits to flowers and plants.

Despite the territorialist behaviour of Phaetornis eurynome, other species of hummingbirds were observed loading pollen on the stigma as well. The other species of hummingbirds did not present the same frequency of visits, and appeared rather to be opportunists despite, although their visits may contribute to the pollination of this species. Whereas P.eurynome approached the flowers directly in a sequential routine, the other species of hummingbirds usually hovered in front of the flowers before collecting nectar, and did not make repeated visits. Stephanoxis lalandi was observed to visit occasionally flowers of V. sparsiflora, and pollen grains of this species was observed in the crest of plumes on the top of the head of an male individual of S. lalandi captured. No other visitors or potential pollinators were observed to visit flowers of this species, despite the massive flowering in the population.

BREEDING SYSTEM: For studies on the breeding system of this species a sample of 13 individuals, which were collected from two natural populations, were transplanted and cultivated at Araras. Hand self- and cross-pollinations were performed with a total of 93 flowers of these plants. Pistils from a sub-sample of such pollinated flowers were fixed at 48, 72, 96, 120, 144 and 168h intervals after pollination for subsequent analysis under fluorescent microscopy. Fruit-set from hand-pollinated flowers was also followed until maturation, and the natural fruit-set was estimated from tagged flowers on different plants of the natural population (Table 5.10.2).

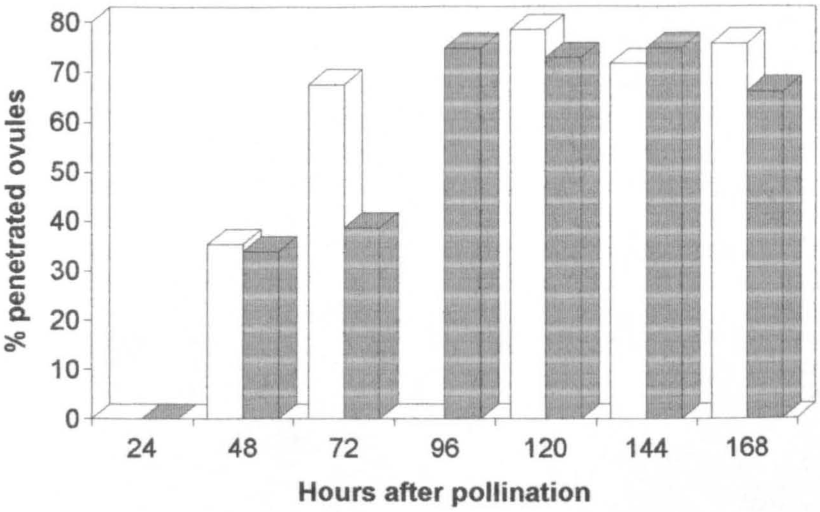
In both cross- and self-pollinated pistils the pollen grains germinated prolifically on the stigma, and a mass of pollen tubes could be distinguished in the style which had reached the ovary by c. 24 hours (N=8); ovule penetration were observed between 24-96 hours and penetrations still accumulated, at least in selfs, over this period apparently. By 48 hours after both self- and cross-pollination, ovule penetration was ca. 30% (N=19), but by 72 hours these was marked difference between ovule penetration in crossed pistils (70%; N=15) and that of selfed pistils (35%; N=10). However, by 120, 144, and 168 hours, there was no significant difference between selfed and crossed pistils (Figure 5.10.1).

Table 5.10.2. Results of experimental hand pollinations treatments with Vriesea sparsiflora var. sparsiflora fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	57.1% (8/14)
selfs	38.9% (N=7/18)
natural fruit-set	54% (27/50)
ISI	0.67

SUMMARY: The endemic Vriesea sparsiflora var. sparsiflora presented a 'steady state' flowering phenology (Gentry, 1974), during the period of September-

Figure 5.10. Vriesea sparsiflora var. sparsiflora: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



48h- SP: mean=34.5% (N=10, range 0-76.6%)
CP: mean=35.5% (N=9, range 0-78.1%)
$P>0.05$

72h- SP: mean=38.8% (N=10, range 0-75.5%)
CP: mean=67.6% (N=15, range 0-84.6%)
$P<0.05$

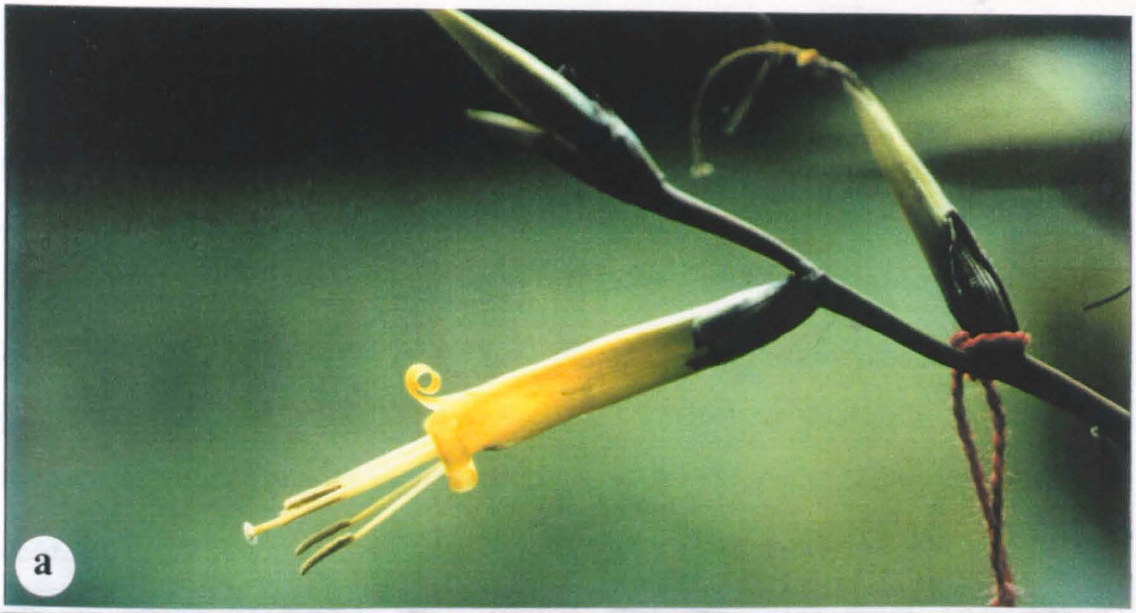
96h- SP: mean=74.7% (N=3, range 69.9-77.1%)

120h- SP: mean=72.7% (N=3, range 69.8-77.1%)
CP: mean=78.4% (N=3, range 72.3-82.7%)
$P>0.05$

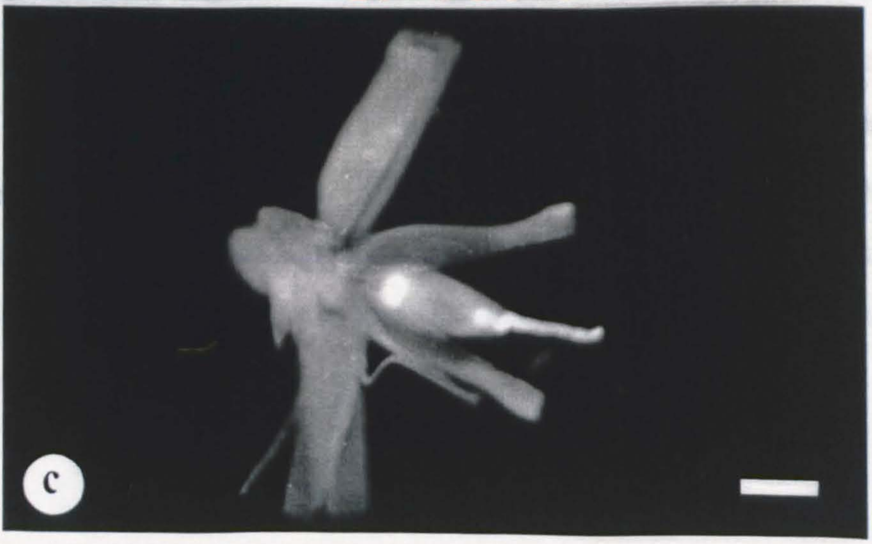
144h- SP: mean=74.8 (N=2, range 73-76.6%)
CP: mean=71.56% (N=3, range 68.4-71.6%)
$P>0.05$

168h- SP: mean=66% (N=3, range 61.5-75%)
CP: mean=75.6% (N=3, range 70.9-84.5%)
$P>0.05$

Plate 5.12. (a) flower of Vriesea sparsiflora var. sparsiflora; (b) inflorescence with open flowers; (c) V. sparsiflora var. sparsiflora - penetrated ovule at 72 h after self-pollination (scale bars = 100μm).


a


b


c

December. It has a diurnal flowering, and is hummingbird pollinated, being visited by *Stephanoxis lalandi*, *Leucochloris albicollis*, and *Clytolaema rubricauda* in the study area. It seems to be self-compatible with fruits developing both from self- and cross-pollination.

BOTANICAL SPECIMENS: Rio de Janeiro State: Nova Friburgo, Ecological Reserve of Macaé de Cima, 18/IX/1986, G.Martinelli 11759 & al. (RB); idem, 30/I/1992, G.Martinelli 14661 & P.Gibbs (RB; cultivated RB, E); idem, 18/X/1992, G.Martinelli 14679 & D.Miller (RB; cultivated RB, E); Macaé, Pico do Frade de Macaé, 09/II/1983, G.Martinelli 9111 & al. (RB); idem, 18/III/1983, G.Martinelli 10641 (RB); idem 16/IX/1982, C.Farney 112 & al. (RB).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Nova Friburgo, Ecological Reserve of Macaé de Cima, 18/X/1992, G.Martinelli 114-ZOO & D.Miller: *Stephanoxis lalandi* (R); idem, 18/X/1992, G.Martinelli 115-ZOO & D.Miller: *Leucochloris albicollis* (R); idem, 17/X/1992, G.Martinelli 111-ZOO & D.Miller: *Phaeornis eurynome* (R).

5.11. ***Quesnelia arvensis*** **(Vellozo) Mez** [Table 5; Figure 5; Plate 5.13,a,b,c,d; 5.14,a,b,c]

MORPHOLOGY: Plant terrestrial or saxicolous with many leaves in a dense rosette. Inflorescence simple, very dense and cylindrical; floral bracts 5cm, exceeding the flowers, rose-coloured. Flowers sessile, 3.5cm long, with free sepals and petals erect with incurved apex, pale-lavender with a blue apex, bearing two serrate appendages at the base; anthers with the connective prolonged, and stigma of the conduplicate-spiral type.

Table 5.11.1. Sequence of the anthesis of Quesnelia arvensis (N=28)

TIME	COROLLA	STAMENS	STYLE	REWARD
06:00	corolla opening; petals with base white and purple to the apex and margins; corolla aperture of 1mm	anthers becoming to release pollen	stigma receptive(?); dusted with pollen	nectar
08:00	corolla aperture of 2mm petals purple with white base	anthers releasing pollen	stigma receptive(?); dusted with pollen	nectar
10:00	corolla aperture of 3-4mm; petals purple	anthers releasing pollen	stigma receptive(?); dusted with pollen	nectar
15:00	corolla aperture 3-4mm; petals purple	anthers becoming empty	stigma receptive(?); dusted with pollen	nectar
17:00	petals turning whitish	anthers empty	stigma receptive(?)	nectar
18:10	corolla closed; petals whitish			no nectar
20:00	corolla closed; petals turning black			no nectar

DISTRIBUTION AND HABITAT: Saxicolous or terrestrial plants on sandy soils or coastal granitic outcrops, near sea level, in 'Restingas' and mangroves of Rio de Janeiro and São Paulo State, in the southeastern sector of the Atlantic Rainforest province. The species was studied in Paraty, Paratymirim, Rio de Janeiro State, at sea level.

FLOWERING PHENOLOGY: The flowering period of Quesnelia arvensis began in June and finished in August, with a synchronized blooming period observed in four populations monitored in the study area. Mature fruits were present in October, when the seeds are dispersed possibly by birds (Figure 5).

The mean number of flowers which opened per day per plant was 8 (N=14, Range 4-12) and the mean number of flowers per inflorescence was 92 (N=10). Flowers at the base of the inflorescence are the first to open such that flowering occurs in a ascending sequence. This species opened 6-14 flowers per day and the availability of the flowers was characterized as 'steady state' (Gentry, 1974).

POLLINATION BIOLOGY: Quesnelia arvensis is a diurnal blooming species and the flowers begin to open at c. 06:00h until 11:00h, with flowers opening successively in this period and lasting until c. 16:00-18:00h.

The development of the anthesis of Quesnelia arvensis did not present any dichogamy between male and female parts. The stamens are included within the corolla and are adnate to the petals, with the longitudinal dehiscence of the anthers introrse to the stigma which is positioned near the base of the anthers. It was observed that soon after the corolla had opened the stigmas were covered with pollen but apparently not receptive (Table 5.11.1)

The inflorescence of this species is very attractive, with floral bracts bright rose and with whitish lanuginous scales at the base. The petals change colour during the anthesis from white with bright-purple on the margins and apex when in bud to rose at base and purple at the apex when open, and pale-lavender to white towards the end of anthesis. A few hours after the completion of anthesis the petals turn black.

The septal nectaries release the nectar by three pores located on the floor of the hypanthium. The petal appendages are fimbriate-serrate, partitioning the corolla into a lower compartment, delineated by the inner hypanthium floor, wall and the petal appendages.

The volume and sugar concentration of nectar was measured in previously bagged inflorescences. The nectar of Quesnelia arvensis presented a mean volume of 28.6μl (N=2, SD±11.6, range 12.3-28.6μl), and mean concentration of sucrose equivalents was 23.8% (N=18, SD±3.63, range 18-29%). Changes in sugar concentration of nectar was observed at the time intervals of 07:00-09:00h and 09:00-11:00h, with the early period of time presenting a higher concentration (27.2% and 21.2%, respectively.

Several different kinds of visitors were observed visiting flowers of Quesnelia arvensis: hummingbirds, birds, bumble bees, bees, butterflies, and even crabs. The hummingbirds were the most important and frequent visitors and seem to be the functional pollinators of this species. Of three different species of hummingbirds, the most frequent were Chlorostylbon aureoventris and Amazilia fimbriata. The first presented a defined pattern of frequency and foraging circuit to the individuals of the population, approaching the flowers from the same general direction and with the same routine. A typical visit by Chlorostylbon aureoventris consisted of a series of visits to the same flowers of the same inflorescence, occasionally intercalating some flowers of other inflorescences, and sucking nectar at almost all flowers of each plant by progressively circling the inflorescence and then flying to another plant. One captured individual of Chlorostylbon aureoventris had a ring like patch of pollen of Quesnelia arvensis at the base of the beak with the head. Amazilia fimbriata, despite of the frequency of its visits to this species, did not present a routine behaviour at the flowers of the individuals visited. Other species of hummingbird, e.g. Chlorestes sp., were observed to visit sporadically a few flowers of Q.arvensis.

All other visitors were seemingly opportunists, visiting the flowers sporadically, and acting as pollen and nectar thieves. The crab (Cesarma sp.) was observed collecting pollen, cutting the petals to gain access to the anthers.

Almost all flowers in the populations of Quesnelia arvensis were infested with a small acarus mite which could be observed in the early stage of the anthesis. In the mist-netted individual of Chlorostylbon aureoventris large quantities of this acarus were found together with pollen of this species.

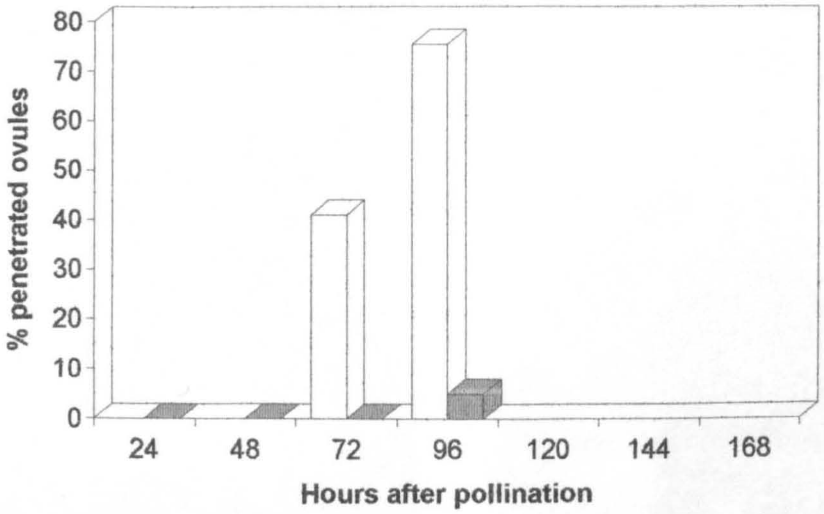
BREEDING SYSTEM: An experimental population consisting of eight individuals was established from plants which were collected in the early stages of flowering from three different natural populations at the study site and cultivated in Araras. Self- and cross-pollinations were performed (N=88). A subsample of hand-pollinated pistils from different treatments were fixed at 72 and 96h after pollination. Fruit-set from the remaining hand-pollination flowers was followed until maturation, and an estimate of natural fruit-set was obtained from tagged flowers in the natural population (Table 5.11.3).

This species seems to be largely self-incompatible although a few fruits developed from self-pollinated pistils. Such fruits were usually smaller in size than those from crossed flowers.

Table 5.11.2. Results of experimental hand-pollinations treatments with Quesnelia arvensis fruit-set and natural fruit-set.

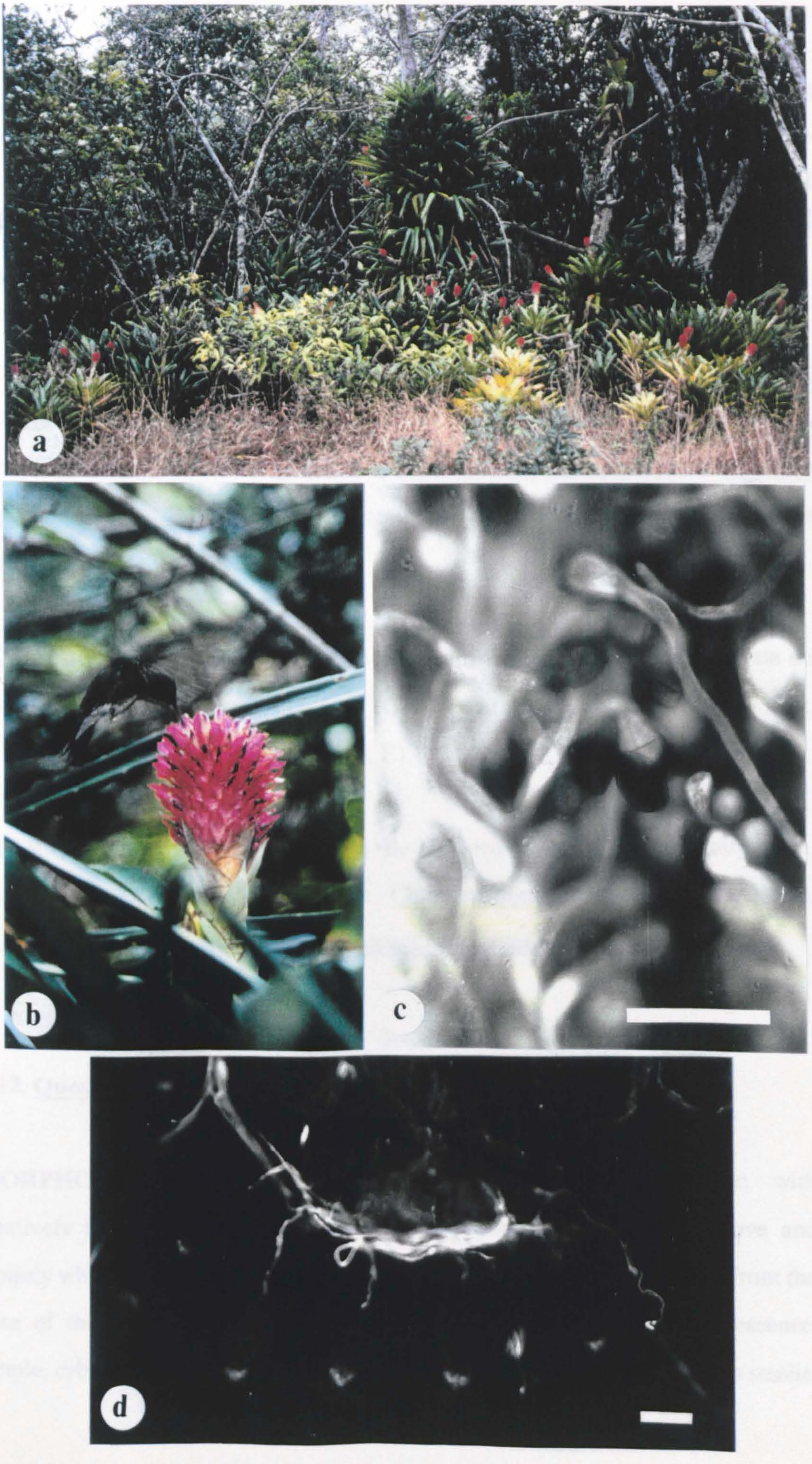
POLLINATION	FRUIT-SET
crosses	70% (7/10)
selfs	20% (2/10)
natural fruit-set	86% (43/50)
ISI	0.28

Figure 5.11. Quesnelia arvensis: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



72h- CP: mean=41% (N=6, range 41.7-72.7%)
96h- SP: mean=5% (N=10, range 0-50%)
CP: mean=75.3% (N=11, range 54.5-89.1%)
$P \leq 0.01$

Plate 5.13. (a) population of Quesnelia arvensis at Paraty; (b) the hummingbird Chlorostilbon aureoventris visiting flower of Q. arvensis; (c) self-pollen grains of Q. arvensis germinating at 24 h after self-pollination (scale bars = 100μm); (d) Q. arvensis - penetrated ovules at 72 h after cross-pollination (scale bars = 100μm)


a
b
c
d

Pollen grains germinated readily during the first 24 hours following cross- and self-pollination, but the self-pollen did not producing pollen tubes into the upper style. The cross-pollen produced mass of pollen tubes which had reached the ovary in pistils fixed at 48 hours, and by 72 hours many tubes had penetrated ovules (Fig. 5.11.1).

SUMMARY:Quesnelia arvensis exhibits a synchronous flowering phenology, during the months of June-September. It has a diurnal flowering, and is hummingbird pollinated, being visited by Chlorostilbon aureoventris and Amazilia fimbriata in the study area. It appears to be self-incompatible, and has a high natural fruit set.

BOTANICAL SPECIMENS: Rio de Janeiro State: Angra dos Reis, Praia do Sul, 02/X/1980, D.Araujo 4137 & al (GUA); Paraty, Paratymirim, 09/IX/1992, G.Martinelli 14699 (RB; cultivated RB, E).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 10/IX/1992, G.Martinelli 204-ZOO: Chlorostylbon aureoventris (R); idem, 12/IX/1992, G.Martinelli 208-ZOO: Amazilia fimbriata (R).

5.12. Quesnelia lateralis **Wawra** [Table 5; Figure 5; Plate 5.15,a,b]

MORPHOLOGY: Plants terrestrial, saxicolous or rarely epiphytic, with relatively few leaves forming a slender, funnelform rosette, green above and densely white-lepidote with transverse bands below; inflorescence lateral from the base of the plant, or sometimes terminal, or with both types of inflorescence, simple, cylindrical; floral bracts equalling the sepals, rose-coloured. Flowers sessile,

Plate 5.14. (a) Quesnelia arvensis - penetrated ovules at 96 h after cross-pollination (scale bars = 100μm); (b) opportunist visits of Bombus sp. to flowers of Q. arvensis; (c) pollen grain germination at 24 h after self-pollination of Q. arvensis pistil (scale bars = 100μm).


a


b


c

with sepals 11-16mm and petals erect, to 33mm, blue, with two fimbriate appendages at base; stamens included at anthesis, and the filaments of the second series highly adnate to the petals; stigma conduplicate-spiral type.

DISTRIBUTION AND HABITAT: Terrestrial, saxicolous or rarely epiphytic plants, in montane wet forest. Endemic to the southeastern sector of the Atlantic Rainforest province, in Rio de Janeiro State. The species was studied in the Ecological Reserve of Macaé de Cima, Nova Friburgo, Rio de Janeiro State.

FLOWERING PHENOLOGY: Quesnelia lateralis presented two pulses of flowering at intervals of 3 months. The first period of flowering in the area of study was between April and May and the second flowering episode occurred in September and October. Fruiting occurs between June and November, respectively, and the seed are dispersed, apparently, by birds. A high number of fruits were predated (Figure 5).

The mean number of flowers per inflorescence was 10 flowers (N=5), and each inflorescence opened synchronously 2-4 flowers per day. Flowers at the base of the inflorescence are the first to open such that flowering occurs in a ascending sequence. The availability of the flowers was characterized as 'cornucopia' (Gentry, 1974).

POLLINATION BIOLOGY: Quesnelia lateralis is a diurnal blooming species, with the flowers opening around 06:00h and lasting for approximately 10 hours. The scape of this species is erect but the inflorescence often hangs downward, sometimes is encountered lying on the soil, due its lateral grow from the base of the plant. The complete sequence of the anthesis is shown in the Table 5.12.1.

Anthesis in Quesnelia lateralis demonstrated a clear dichogamy with marked protandry. In the early hours of the anthesis, the conduplicate-spiral stigma is not receptive and is located at c. half the height of the anthers, but the style gradually extends to that stigma is c. 3mm above the apex of the anthers, nearly 3-4 hours later, at which time the stigma is receptive (see Table 5.12.1).

The colour of the floral bracts and petals seems to be the most attractive advertisement to the pollinators. The floral bracts are bright red or rose, making a strong contrast with the bright blue of the petals. When in bud the petals are pale blue but they change to bright blue at anthesis.

The nectar is presented by three nectar-release pores located on the floor of the hypanthium. The petal appendages are fimbriate and cut off a lower intrafloral chamber formed by the inner hypanthium floor, wall, and the petal appendages.

The volume and sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The production of nectar in Quesnelia lateralis is moderate, with the mean volume of nectar per flower of 11.7μl (N=3, SD±5.16, range 7.7-17.5μl) and mean of concentration of sucrose equivalents of 30.5% (N=11, SD±3.08, range 24-36%).

No pollinators were observed visiting this species despite several hours of observations on various days. Q. lateralis is most likely to be pollinated by hummingbirds.

BREEDING SYSTEM: An experimental population was created comprising eight plants, which were collected in the early stages of flowering from two different natural populations, and were cultivated in Araras. Hand-pollinations (N=78) were performed with previously bagged flowers of this artificial population and hand-pollinated pistils from different treatments were fixed at 24, 48 and 72 hours post pollination. Fruit-set from the remaining hand-pollinated flowers was followed until maturation, and an estimate of natural fruit-set was obtained from tagged flowers (N=50) on different plants of the natural population.

Table 5.12.1. Sequence of the anthesis of Quesnelia lateralis (N = 10).

TIME	COROLLA	STAMENS	STYLE	REWARD
06:00	corolla opening	anthers beginning to release pollen	stigma at the half length of the anthers, not receptive	releasing nectar
08:00	corolla open	anthers releasing pollen	stigma 2mm above the apex of the anthers, becoming receptive	releasing nectar
10:00	corolla open	anthers releasing pollen	stigma 3mm above the apex of the anthers, receptive	releasing nectar
16:30	corolla closing	anthers empty	stigma dry, not receptive (?)	not releasing nectar

This species seems to be self-incompatible. In both self- and cross-hand-pollinations experiments the pollen grains germinated prolifically on the stigma and a mass of pollen tubes could be distinguished in the style, which reached the ovary and penetrated the ovules in 48 hours after pollination. Selfed pollen grains also germinate in the stigma but did not produce pollen tubes (Fig. 5.12.1). Most self-pollinated pistils failed to set fruit and the natural fruit-set was low (Table 5.12.2).

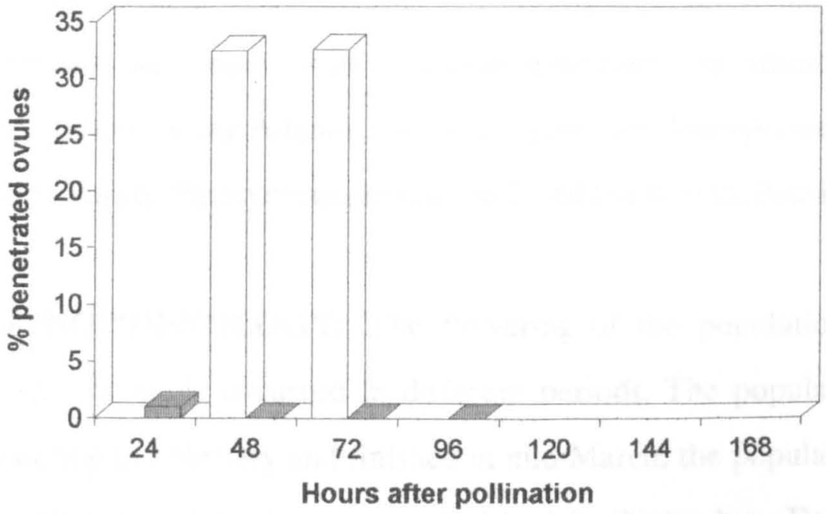
Table 5.12.2. Results of experimental hand-pollination treatments with Quesnelia lateralis fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	80% (8/10)
selfs	7.6% (1.13)
natural fruit-set	44% (22/50)
ISI	0.09

SUMMARY: Quesnelia lateralis exhibits 'cornucopia' flowering phenology, in two distinct periods, during the months of April-May, and September-October. It has a diurnal flowering, and is most likely to be pollinated by hummingbirds or perhaps butterflies. It appears to be self-incompatible, and has a relatively low natural fruit-set.

BOTANICAL ESPECIMENS: Rio de Janeiro State: Santa Maria Madalena, 24/VI/1987, T.Wendt 150 & al. (RB); Petrópolis, Fazenda Inglesa, 27/VII/1978, G.Martinelli 4854 (RB); Morro da Bandeira, 01/VII/1985, C.Farney 769 & al. (RB); Itaipava, 24/IV/1977, G.Martinelli 1653 (RB); idem, 23/IV/1980, G.Martinelli 6737 & T.Plowmann (RB); idem, Mata do Facão, 25/IV/1986, G.Martinelli 11571 (RB); Nova Friburgo, Ecological Reserve of Macaé de Cima, 18/IX/1986, G.Martinelli 11755 (RB); idem, 15/IV/1992, G.Martinelli 14684 (RB;cultivated RB, E).

Figure 5.12. Quesnelia lateralis: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



24h- SP: mean= 1% (N=7, range 0-7%
48h- CP: mean=32.5% (N=5, range 0-82%)
72h- CP: mean=27.2% (N=6, range 0-85%)

5.13. Pitcairnia flammea Lindley var. flammea [Table 5; Figure 5; Plate 5.15,c,d; 5.16,a,b]

MORPHOLOGY: Plant saxicolous with a bulbous-thickened base, and few leaves, all alike and up to 1m. Inflorescence simple, red; floral bracts red, shorter than the flowers. Flowers suberect to spreading, pedicels slender; sepals red and petals 6cm, without appendages, red, with the stamens included, ovary 2/3 superior, stigma conduplicate-spiral type.

DISTRIBUTION AND HABITAT: Saxicolous, usually on granitic outcrops, especially by streams or wet, rocky places, from sea level to 1800m, in lowland wet forest, montane wet forest, high montane grassland and granitic outcrops of southeastern sector of the Atlantic Rainforest province. The species was studied at two sites: (a) Paraty, Paratymirim, at sea level, and (b) Araras, Petrópolis, 1000m.

FLOWERING PHENOLOGY: The flowering of the populations at the two different sites of study occurred in different periods. The population of Paraty began flowering in February and finished in mid-March; the population of Araras, came into flower in late August and finished in September. Fruiting in these populations occurred in April and in October, respectively.

The mean number of flowers per inflorescence was 15 (N=24). The individuals of both areas flowered rather asynchonously, with plants flowering successively, and so with a non-defined peak of flowering. Each individual plant flowers over a period of 2-6 days, with 3-6 flowers per day. The availability of the flowers was determined as 'steady state' (Gentry, 1979).

POLLINATION BIOLOGY: Pitcairnia flammea var. flammea is a diurnal flowering species, and the flowers begin to open around 06:00h until 10:00h. As flowering proceeds the petals move to one side, over the anthers, and so form a

Table 5.13.1. Sequence of the anthesis of Pitcairnia flammea var. flammea (N = 16).

TIME	COROLLA	STAMENS	STYLE	REWARD
06:00	corolla opening; petals converging for one side and exposing a lateral aperture	anthers releasing pollen	stigma at the same length of the apex of anthers, dry not receptive	nectar
08:00	corolla open; petals converged for one side over the anthers, exposing the anthers and stigma; petals slightly recurved	anthers releasing pollen	stigma 2mm above the apex of the anthers; not receptive	nectar
10:00	corolla open	anthers releasing pollen	stigma 4mm above the apex of the anthers, not receptive	nectar
12:00	corolla open	anthers releasing pollen	stigma 10mm above the apex of the anthers, receptive	nectar
15:00	corolla beginning to close, twisting and enfolding the stamens and style, with just the stigma exserted	anthers empty	stigma becoming dry, not receptive	little nectar
16:00	corolla closed		stigma exserted, dry, not receptive	no nectar

lateral aperture that increases gradually in size. The duration of the anthesis is approximately 10 hours (Table 5.13.1).

Flowers of Pitcairnia flammea var. flammea show dichogamy with marked protandry. In the early hours of the anthesis, the stigma is not receptive and is located at the same height as the apex of the anthers. It gradually develops to reach a height of 10mm above the apex of the anthers some 5 hours later, when the stigma became receptive (see Table 5.13.1).

The inflorescence and the flowers of this species are very attractive, with a conspicuous bright red in all parts. The septal nectaries release the nectar by pores located at the base of gynoecial suture. There are no petal appendages in this species, but the lack of these structures is perhaps compensated for by the zygomorphic development of the corolla which may aid the retention of nectar.

The sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The volume of nectar of a single flower of Pitcairnia flammea var. flammea at 12:40h was 30.7μl (N=1), and mean of concentration of sucrose equivalents of 17.4% (N=9, SD±4.72, range 11-25%). Changes in sugar concentration of nectar were observed between the time intervals of 06:00-10:00h and 12:00-16:00h with the later period of time presenting higher sugar concentration, (17% and 20.1% respectively), which coincides with the time of receptivity of the stigma.

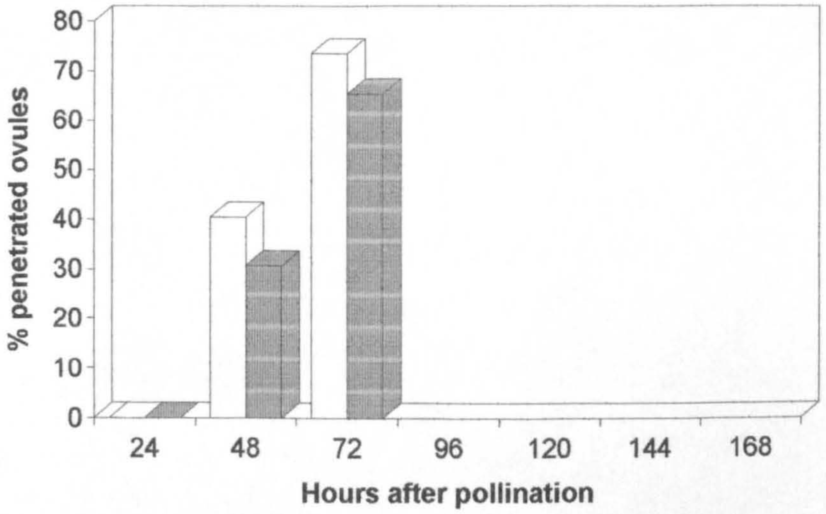
The visitors of Pitcairnia flammea var. flammea were hummingbirds in both areas of study. In the population at Petrópolis, the most frequent visitor was Phaetornis eurynome, with a well-defined pattern of frequency of visits on the individuals of the populations, approaching the plants and flowers from the same general direction and with almost the same routine. A typical visit of Phaetornis eurynome consisted in a series of repeated visits to the same flower, with intervals varying between 6 to 20 minutes, subsequently visiting at least 2-3 others flowers of each inflorescence. At each flower, P.eurynome expended less than one second sucking nectar. The head of the hummingbird contacted first the stigma when introducing the beak into the flowers and when leaving the flower. Another visitor was Melanotrochilus fuscus, which made sporadic visits to a few flowers. Meliponideae bees were also frequent during morning periods, when they attempted to gain access the nectar via the narrowed tube formed by the petals.

At the Paraty population, the visitors were the hummingbirds Amazilia fimbriata, which visited few flowers, rather sporadically, and Phaetornis aff. petrei which presented a well defined behaviour with regard to frequency, routine, and also with a territorialist behaviour. Meliponid bees were also observed visiting the flowers as nectar thieves, gaining access to nectar via the base of the corolla aperture.

BREEDING SYSTEM: An experimental population comprising 24 plants which were collected at an early stage of flowering from the two different natural populations was cultivated at Araras. Self- and cross-pollinations were performed in previously bagged flowers (N=81). A subsample of hand pollinated pistils from different treatments were fixed at 48 and 72 hours after pollination. Fruit-set from the remaining hand-pollinated flowers was followed until maturation, and an etimate of natural fruit-set was obtained from tagged flowers from different plants of both natural populations.

P.flammea var. flammea seems to be self-compatible although crossed flowers were rather more successful at fruit set. Fig. 5.13.1, shows the results of hand-pollinated flowers. The pollen grains germinated readily following cross- and self-pollinations during the first 24 hours, and both produced masses of pollen tubes that had reached the ovary in pistils fixed at 48 and 72 hours (see Fig. 5.13.1), although the incidence of penetrated ovules was greater in crossed pistils at these time intervals.

Figure 5.13. Pitcairnia flammea var. flammea: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



48h- SP: mean=30.6% (N=5, range 15.4-57.9%)
CP: mean=40.4% (N=5, range 0-74.5%)
P>0.05

72h- SP: mean=65.3% (N=7, range 42.8-75.7%)
CP: mean=73.5% N=5, range 66.4-86.1%)
P>0.05

Plate 5.15. (a) inflorescence and (b) flowers of Quesnelia lateralis; (c) Pitcairnia flammea var. flammea - penetrated ovule at 96 h after self-pollination (scale bars = 100μm); (d) pollen grain germination at 24 h after self-pollination of pistil of P. flammea var. flammea (scale bars = 100μm).

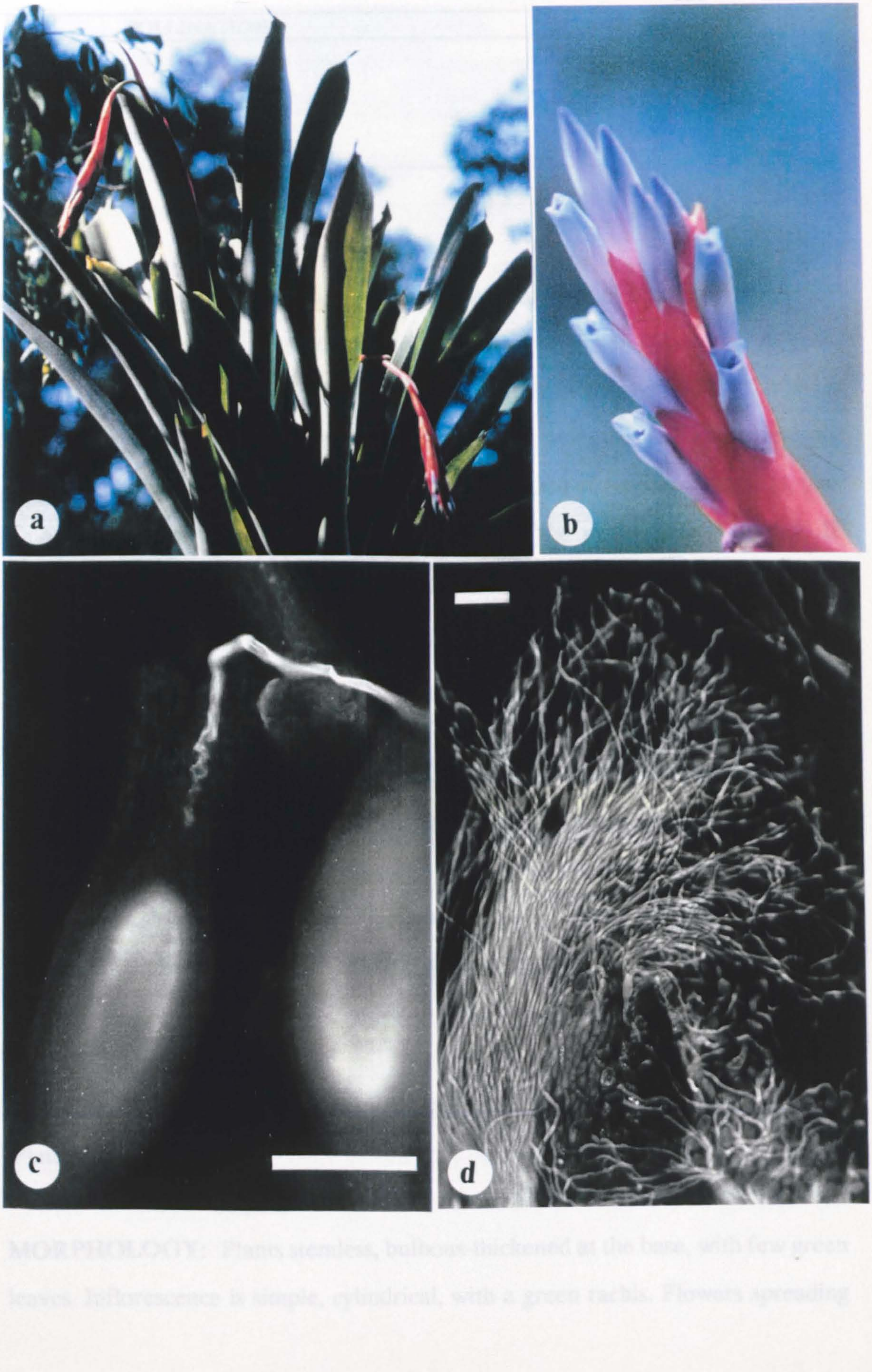

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Table 5.13.2. Results of experimental hand-pollinations treatments with Pitcairnia flammea var. flammea fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	86.1% (31/36)
selfs	66.7% (10/15)
natural fruit-set	82% (41/50)
ISI	0.77

SUMMARY:Pitcairnia flammea var. flammea flowers during the months of February and March in the study area of Paraty, at sea level, and during August-September in the area of study of Araras, Petropolis, at 1000 m of altitude. It has a diurnal flowering, and is hummingbird-pollinated, being visited by Phaetornis eurynome and Melanotrochilus fuscus in the population of Araras, Petropolis, and by Amazilia fimbriata and Chlorestes notatus in the population of Paraty. It appears to be self-compatible, and has a high natural fruit-set.

BOTANICAL SPECIMENS: Rio de Janeiro State: Petrópolis, 09/VI/1978, G.Martinelli 4569 (RB); idem, Morro do Cuca, 26/IX/1977, G.Martinelli 3085 (RB); Paraty, Paratymirim, 13/II/1992, G.Martinelli 14685 (RB; cultivated RB, E); Petrópolis, Araras, 14/VIII/1992, G.Martinelli 14737 (RB; cultivated RB, E).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Petrópolis, Araras, 14/II/1992, G.Martinelli 211-ZOO: Phaetornis eurynome (R).

5.14. Pitcairnia flammea Lindley var. pallida L.B.Smith [Table 5; Figure 5; Plate 5.16,c; 5.17,a,b,c,d]

MORPHOLOGY: Plants stemless, bulbous-thickened at the base, with few green leaves. Inflorescence is simple, cylindrical, with a green rachis. Flowers spreading with sepals green; petals 7 cm, naked, yellowish-white turning white at anthesis; the stamens are included; stigma conduplicate-spiral.

DISTRIBUTION AND HABITAT: Saxicolous plants, always in rocky areas besides shady streams, between 900-1200m. Endemic to the montane wet forest of southeastern sector of the Atlantic Rainforest province. The species was studied in the Serra dos Órgãos National Park, Teresópolis, Rio de Janeiro State.

FLOWERING PHENOLOGY: The endemic var. pallida of the species Pitcairnia flammea flowers in October (Figure 5). Each plant flowers for c. four days, and since flowering was not particularly synchronous, the whole period of the flowering of the population was c. 25-30 days. The availability of flowers of P. flammea var. flammea was characterized as 'cornucopia' (Gentry, 1974).

Each plant opened 3-4 flowers per day and the mean number of flowers per inflorescence was 18 (N=30). Flowers at the base of the inflorescence are the first to open such that flowering occurs in a ascending sequence.

POLLINATION BIOLOGY: The species is crepuscular to night-blooming, and the flowers began to open between 15:00-16:00h, when the petals converge to one side, over the anthers and the stigma, forming a lateral aperture that increases in size graually during the early hours of anthesis (Table 5.14.1).

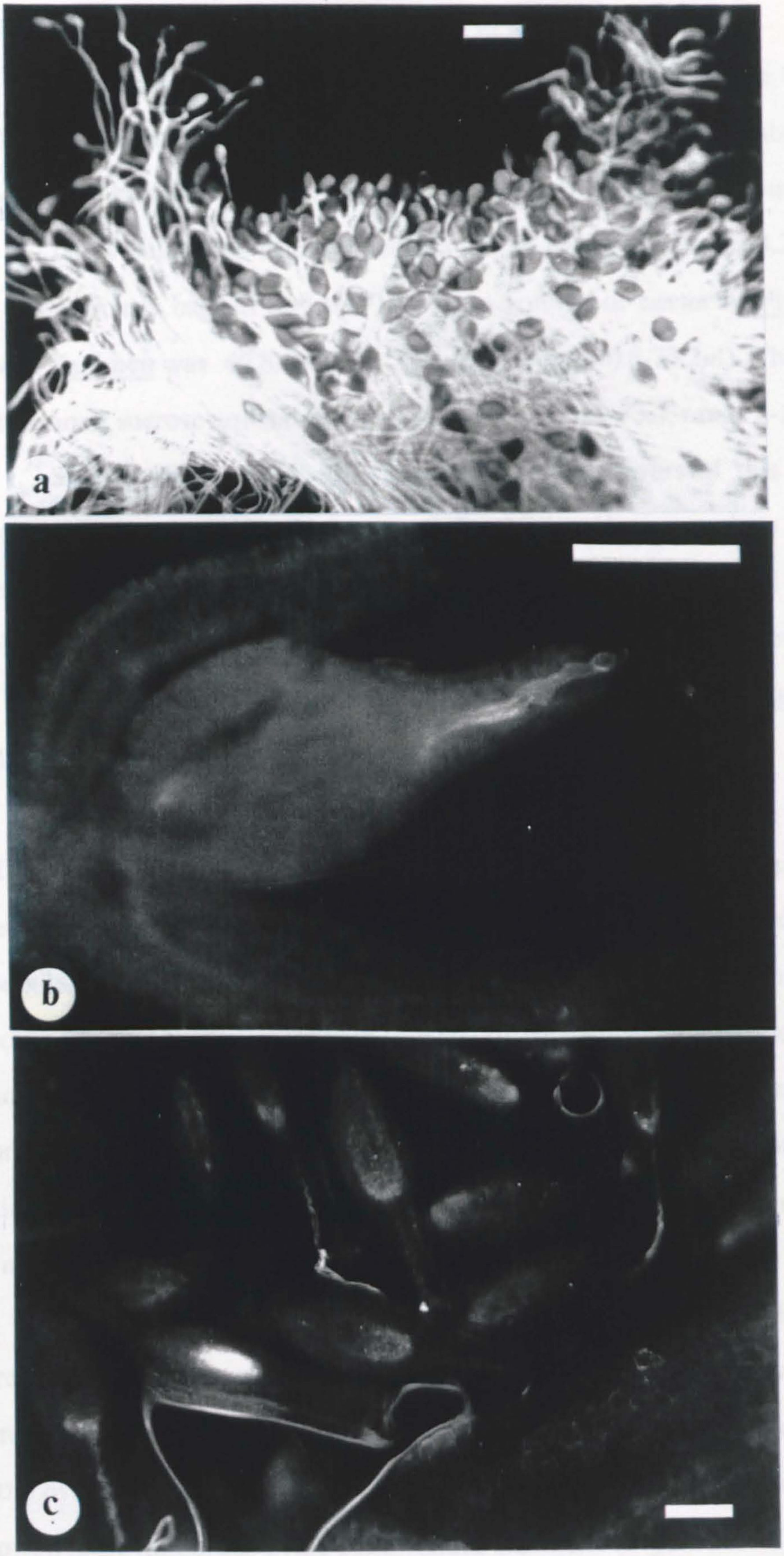
In Pitcairnia flammea var. pallida the flowers are dichogamous with marked protandry. In the early hours of the anthesis, the stigma is localized at 2mm above the apex of the anthers, and with gradual extension of the style reaches 6-8mm above the apex of the anthers, some 3 hours later. The duration of the anthesis is approximately eight hours (see Table 5.14.1).

The white colour of the petals, and the sweet fragrance of the flowers of P.flammea var. pallida, which is usually evident 3-4 hours after the

Table 5.14.1. Sequence of the anthesis of Pitcairnia flammea var. pallida (N=6)

TIME	COROLLA	STAMENS	STYLE	REWARD
16:00	corolla opening; petals converging to one side and forming a lateral aperture	anthers releasing pollen	stigma at same height of the apex of the anthers, not receptive	nectar
18:00	corolla open by an lateral aperture formed by the convergent petals	anthers releasing pollen	stigma 3mm above the apex of the anthers, receptive (?)	nectar
20:00	corolla open; accented sweet smell	anthers releasing pollen	stigma 6-7mm above the apex of the anthers, receptive	nectar
22:00	corolla open; accented weet smell	anthers releasing pollen	stigma 7-8mm above the apex of the anthers, receptive	nectar
02:00	corolla becoming to close; not smelling	anthers empty	stigma 8mm above the apex of the anthers, becoming not receptive	nectar

Plate 5.16. (a) *Pitcairnia flammea* var. *flammea* - pollen grains germination at 96 h after self-pollination (scale bars = 100μm); (b) penetrated ovule of *P. flammea* var. *flammea* at 48 hours after self-pollination (scale bars = 100μm); (c) penetrated ovules of *Pitcairnia flammea* var. *pallida* at 96 h after self-pollination (scale bars = 100μm).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opening of the corolla, (which coincides with the period of receptivity of the stigma) seem to be the most important attractants to the pollinator.

The septal nectaries release nectar via pores located at the base of gynoecial suture. The partial zygomorphism of the corolla can be hypothesized as a substitution for the lack of the petal appendages in order to nectar retention.

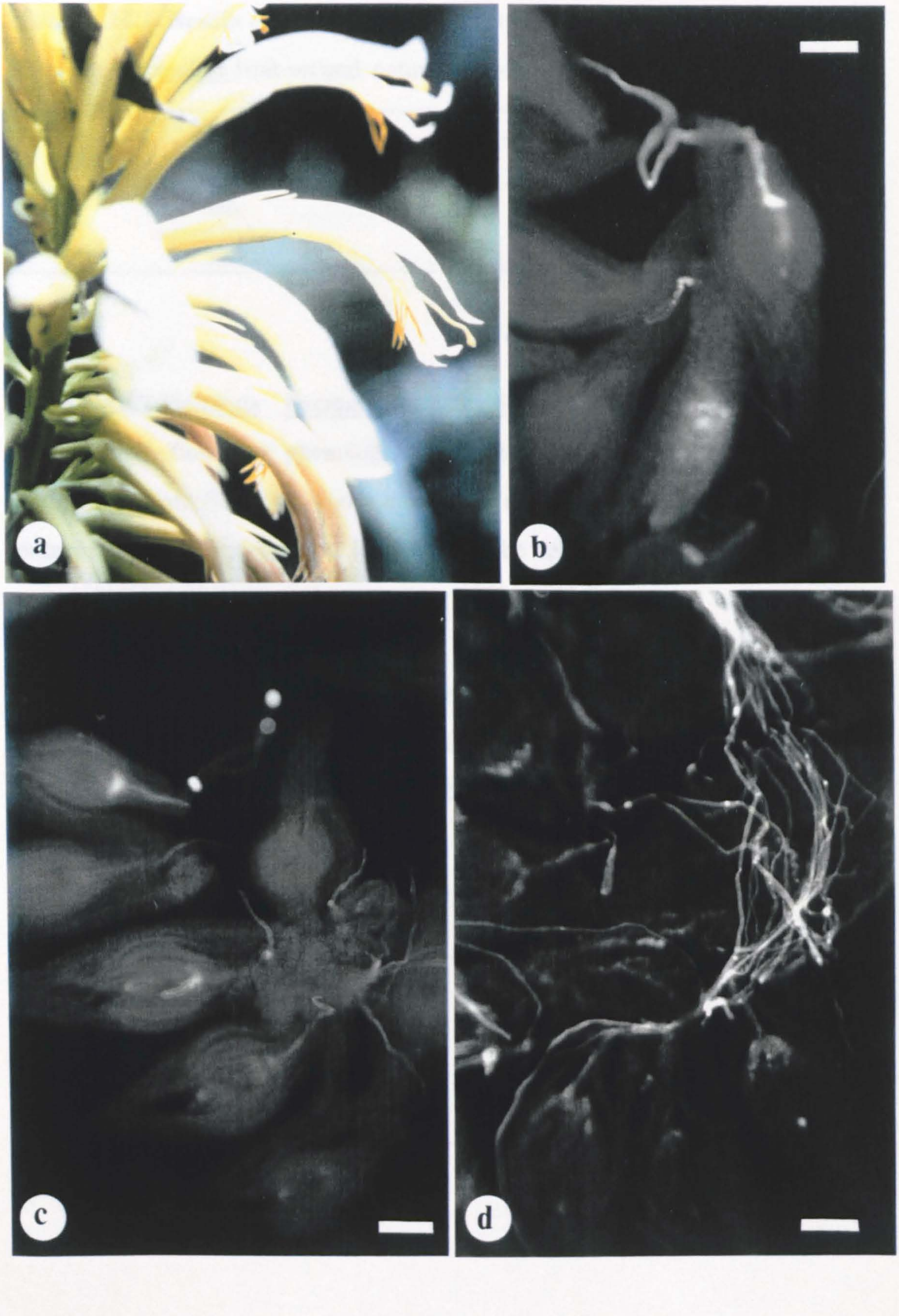
The volume and sugar concentration of nectar (Table 5.14.2) were measured in previously bagged flowers. The mean volume of nectar of Pitcairnia flammea var. flammea was 60.8μl (N=6, SD±6.03, range 40.8-73.2μl). The mean of concentration of sucrose equivalents was 12.7% (N=6, SD±3.4, range 8-19%).

Shortly after opening (in crepuscular light) flowers of this species were visited by the hummingbird Melanotrochillus fuscus. However, since flowers are markedly dichogamous, the stigma were not receptive at this time, and it is not known wheter flowers were effectively pollinated by the hummingbird. No nocturnal visitor were observed, but it is possible that P. flammea var. pallida is pollinated by nocturnal hawkmoths (Sphingidae).

BREEDING SYSTEM: An experimental population comprising a sample of five plants which were collected in the early stage of flowering from two different natural populations was cultivated at Araras. Self- and cross-pollinations were performed in previously bagged flowers (N=60). A subsample of hand-pollinated pistils from different treatments were fixed at 24, 48, 72 and 96 hours after pollination. Fruit-set from hand-pollinated flowers was followed until maturation, and a estimate of natural fruit-set was obtained from tagged flowers of different plants of natural population (Table 5.14.2).

Fluorescence microscopy analysis of the hand-pollinations demonstrated that in both cross- and self-pollinations, the pollen grains germinated readily on the stigma by 24 hours, and both treatments produced pollen tubes that reached the ovary by 48 hours. However, over the time intervals of 48-97h, crossed pistils showed more numerous ovule penetrations than selfs (Figure 5.14.1).

Plate 5.17. (a) flowers of Pitcairnia flammea var. pallida; (b) penetrated ovules of P. flammea var. pallida at 48 h after self-pollination (scale bars = 100μm); (c) penetrated ovules of P. flammea var. pallida at 72 h after self-pollination (scale bars = 100μm); (d) penetrated ovules of P. flammea var. pallida at 72 h after self-pollination (scale bars = 100μm).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c
d

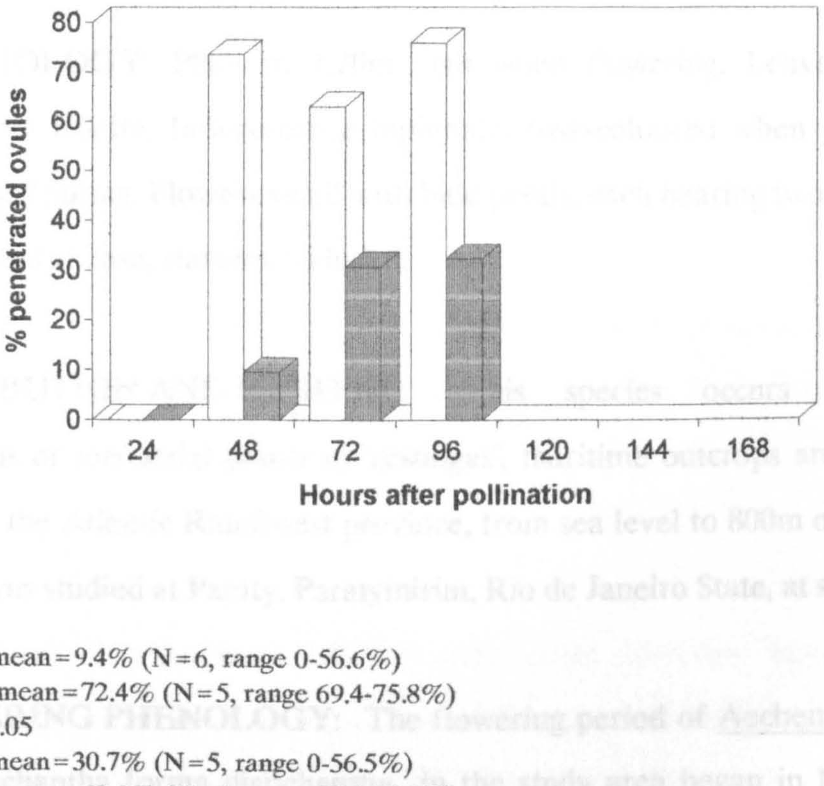
Table 5.14.2. Results of experimental hand-pollinations treatments with Pitcairnia flammea var. pallida fruit-set and natural fruit-set.

POLLINATION	FRUIT-SET
crosses	86.1% (31/36)
selfs	66.7% (10/15)
natural fruit-set	82% (41/50)
ISI	0.77

SUMMARY: Pitcairnia flammea var. pallida exhibits a very brief and characteristic flowering phenology, during the month of October. It has a crepuscular-night flowering, and is most likely to be pollinated by hawkmoths and occasionally by hummingbirds. It appears to be self-compatible, and has a high natural fruit-set.

BOTANICAL SPECIMENS: Rio de Janeiro State: Teresópolis, Serra dos Órgãos National Park, 21/X/1977, G.Martinelli 3334 (RB); idem, 17/IX/1983, G.Martinelli 9303 (RB); idem, 14/X/1992, G.Martinelli 14705 (RB; cultivated RB, E).

Figure 5.14. Pitcairnia flammea var.pallida: incidence of penetrated ovules in pistils fixed at intervals after hand cross- (white-bars) vs. self pollination (hatched bars).



48h- SP: mean=9.4% (N=6, range 0-56.6%)
CP: mean=72.4% (N=5, range 69.4-75.8%)
$P<0.05$

72h- SP: mean=30.7% (N=5, range 0-56.5%)
CP: mean=62.8% (N=5, range 38.1-73.2%)
$P<0.05$

96h- SP: mean=32.4% (N=5, range 0-56.7%)
CP: mean=68.4% (N=5, range 58.2-86.5%)
$P<0.05$

SECTION B:

5.15. Aechmea distichantha Lemaire var. distichantha forma distichantha

[Table 5; Figure 5; Plate 5.18,a]

MORPHOLOGY: Plant to 1.20m high when flowering. Leaves in a dense, funnelform rosette. Inflorescence bipinnate, rose-coloured when young and red during the fruiting. Flowers small with blue petals, each bearing two oblong serrate appendages at base, stamens included.

DISTRIBUTION AND HABITAT: This species occurs as epiphytic, saxicolous or terrestrial plants in 'restingas', maritime outcrops and lowland wet forest of the Atlantic Rainforest province, from sea level to 800m of altitude. The species was studied at Paraty, Paratymirim, Rio de Janeiro State, at sea level.

FLOWERING PHENOLOGY: The flowering period of Aechema distichantha var. distichantha forma distichantha in the study area began in November and finished in December and mature fruits occurred between January and February (Figure 5). This species has diurnal flowers with the anthesis beginning around 07:00h.

POLLINATION BIOLOGY: When the flowers opens, the anthers are already releasing pollen, and the stigma, which seems to be receptive, is located at the same height of the anthers.

The bright rose colour of the inflorescence and the contrasting blue petals appear to be the most important advertisement for the pollinator. Due the small size of the flowers and difficult access to the flowers, data on the volume and concentration of nectar was not obtained. The hummingbirds Ramphodon naevius and Thalurania glaucopsis were the visitors of this species.

BREEDING SYSTEM: Hand-pollinations experiment with previously bagged flowers were performed with two individuals collected in the natural population and transplanted to Araras. Only self-pollinations were possible. The pistils from self-pollinations were fixed at 24, 48, and 72 hours after anthesis and were analysed under fluorescence microscopy.

The analysis of the selfed pistils (N=6) showed that the self-pollen grains germinated on the stigma but did not form pollen tubes at any of the time intervals, suggesting that this species is self-incompatible. Future experiments with a larger sample, and with control cross-pollinations, would be necessary to determine this with certainty.

SUMMARY: This species exhibits 'steady state' flowering phenology, during November and December and has diurnal flowers. It is hummingbird-pollinated, being visited by Ramphodon naevius and Thalurania glaucopsis and seems to be self-incompatible with the site of self-incompatibility in the stigma, but higher number of sample and future investigations would be required.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 14/XII/1992, G.Martinelli 14789 (RB, cultivated RB).

5.16. Aechmea fasciata (Lindley) Baker var. fasciata [Table 5; Figure 5; Plate 5.18,b,c]

MORPHOLOGY: Plant propagating by rhizomes, some 60cm high when flowering; leaves forming a cylindric rosette. Inflorescence with floral bracts rose, white-flocculose, at anthesis; flowers sessile, polystichous, with petals purple turning red after anthesis, bearing two fimbriate appendages at base; stamens included, with the filaments of the second series highly adnate to the petal.

DISTRIBUTION AND HABITAT: This epiphytic species is endemic to the lowland and montane wet forest of the Atlantic Rainforest province, between 200 and 1300m of altitude, in the Rio de Janeiro State. The species was studied at Fazenda Inglesa, Petrópolis, Rio de Janeiro State, at 900m of altitude.

FLOWERING PHENOLOGY: The flowering period of Aechmea fasciata var. fasciata began in December and finished in January. Fruiting occurred in February and early March and dispersion seems to be zoochorous (Figure 5). This species appears to be day-blooming and the anthesis began at 05:30h.

POLLINATION BIOLOGY: Anthesis of Aechmea fasciata var. fasciata showed that the anthers released pollen just prior to flower opening, when the stigma was seemingly receptive, and nectar was also present. At the onset of anthesis, the petals were purple and gradually changed to red.

The rose and white-flocculose inflorescence, with the rose floral bracts and the purple corolla, seems to be the principal advertisement for the pollinator. The volume and sugar concentration of nectar of this species (Table 5) was measured in previously bagged flowers. The maximum volume of nectar in a single flower was 15.6μl (N=1) and the mean concentration of sucrose equivalents was 28% (N=7, SD±2.34, range 22-32%). The visitor of A.fasciata var. fasciata was an unidentified hummingbird, which contacted the stigma during the visits.

BREEDING SYSTEM: During the period of field research of this study, it was possible to collect only two flowering individuals from the same cluster to cultivated, thus limiting the experiments to self-pollinations. The self-pollination experiment was performed in previously bagged flowers (N = 12) and all were fixed at 24, 48 and 72 hours after anthesis.

The self-pollinated pistils showed that the pollen grains germinated on the stigma but did not form pollen tubes in the style, suggesting that this species is self-incompatible. A larger sample of flowers and individuals would be necessary to determine this with certainty.

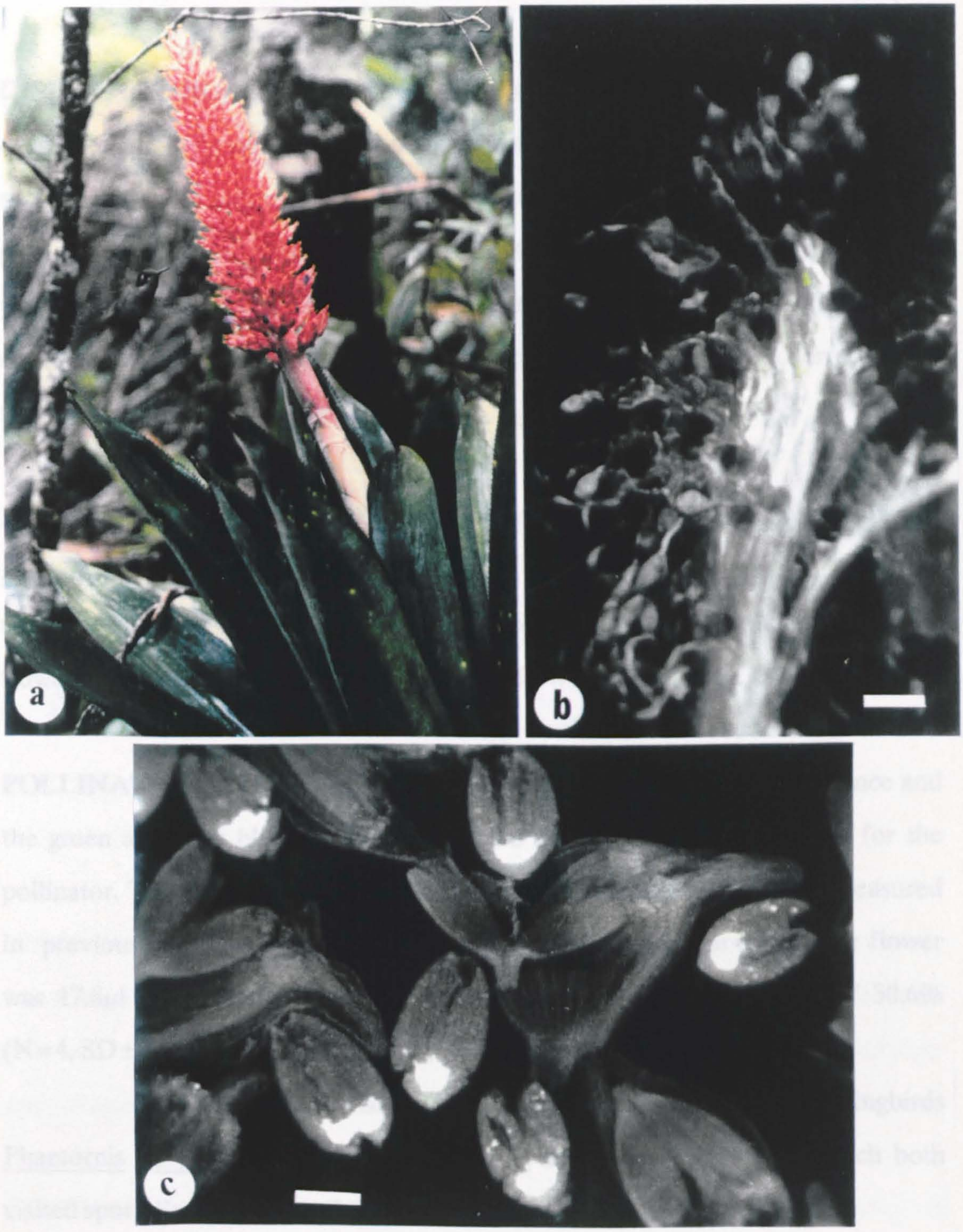
SUMMARY: The flowering of Aechema fasciata var. fasciata in the study area was December and January, and this species seems to be pollinated by hummingbirds. The preliminary experiments results suggest that this species is self-incompatible with the site of incompatibility in the stigmatic head.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Petrópolis, Fazenda Inglesa, 22/I/1993, G.Martinelli 14793 (RB, cultivated RB, E).

5.17. Billbergia amoena (Loddiges) Lindley var. amoena [Table 5; Figure 5]

MORPHOLOGY: Plant propagating by short or spreading rhizomes, to 60cm high when flowering. Inflorescence usually compound but sometimes simple, primary bracts dark red. Flowers with sepals and petals green and dark blue apex,

Plate 5.18. (a) the hummingbird Thalurania glaucopsis approaching the inflorescence of Aechmea distichantha var. distichantha; (b) pollen grains germinating of Aechmea fasciata var. fasciata at 72 h after self-pollination (scale bars = 100μm); (c) not penetrated ovules of A. fasciata var. fasciata at 72 h after self-pollination (scale bars = 100μm);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each petal bearing two fimbriate appendages at base. Stamens are initially included with the flower, but the petals soon recurve and expose them.

DISTRIBUTION AND HABITAT: This species is very widespread, and occurs as epiphytic or terrestrial plants, from sea level to 1200m of altitude, in restingas, granitic outcrops, lowland and montane wet forest, and high montane grasland, as well as other types of vegetation of different phytogeographical provinces from Bahia to Santa Catarina States. The species was studied in Macaé de Cima Ecological Reserve, Nova Friburgo, where it occurs as a terrestrial in montane wet forest, at 1100m of altitude.

FLOWERING PHENOLOGY: The flowering period of Billbergia amoena var. amoena occurred in October and the fruiting occurred in November. This species showed a 'cornucopia' type of flowering phenology with all plants coming to flower over a priod of 6-8 days. It has diurnal flowers, which open c. 06:30h

POLLINATION BIOLOGY: The red primary bracts of the inflorescence and the green and dark blue flowers seem to be the principal advertisement for the pollinator. The volume and sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The maximum volume of nectar in a single flower was 17.6μl N=1) and the mean concentration of sucrose equivalents of 30.6% (N=4, SD±2.19, range 23-32%).

The principal visitors of this species were the hummingbirds Phaetornis eurynome, Clitolaema rubricauda and Heliothryx aurita, which both visited sporadically flowers of the individuals monitored in the study area.

BREEDING SYSTEM: An experimental population was created with a sample of three individuals which were collected in the natural population and cultivated in Araras, Petrópolis. Only one individual flowered, limiting the hand-pollination experiments to self-pollination treatments, and the selfed pistils were fixed at 72 hours after pollination.

Billbergia amoena var. amoena seems to be self-compatible with the self-pollen grains germinating freely on the stigma, and with penetrated ovules at 72 hours interval (mean 27%, N=5, range 0-54.8%).

SUMMARY: This species flowered during the month of October, presenting a 'cornucopia' phenological type and has a diurnal flowering, being visited by the hummingbirds Clitolaema rubricauda and Heliothryx aurita.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Macaé de Cima Ecological Reserve, Nova Friburgo, 30/XI/1992, G.Martinelli 14700 (RB; cultivated RB, University of St.Andrews).

5.18. Billbergia pyramidallis (Sims) Lindley var. pyramidallis

[Table 5; Figure 5; Plate 5.19,a,b]

MORPHOLOGY: Leaves few in a tubular rosette. Inflorescence with primary bracts bright rose-coloured, massed beneath the inflorescence. Flowers with sepals pale red, and petals red with a blue apex, each petal bearing two fimbriate appendages at base. Stamens just included in the corolla.

DISTRIBUTION AND HABITAT: Terrestrial or epiphytic plants in restingas, and lowland and montane wet forest of the Atlantic Rainforest province, and also occurring in Cuba and Venezuela, from sea level to 1700m of altitude. This species was studied in Macaé de Cima Ecological Reserve, Nova Friburgo, Rio de Janeiro State where it occurs as a terrestrial or epiphyte in montane wet forest, at 1000m of altitude, and Araras, Petrópolis where occurs as terrestrial in montane wet forest, at 800m of altitude.

FLOWERING PHENOLOGY: The flowering period of Billbergia pyramidallis var. pyramidallis in Macaé de Cima Ecological Reserve was in September, and in the population of Araras, Petrópolis in December (Figure 5). Fuiting occurred in October and January respectively. The mean number of flowers per inflorescence was 15.2 (N=5). The species opened 6-8 flowers per day with anthesis beginning c. 06:00h and finishing around 16:00h.

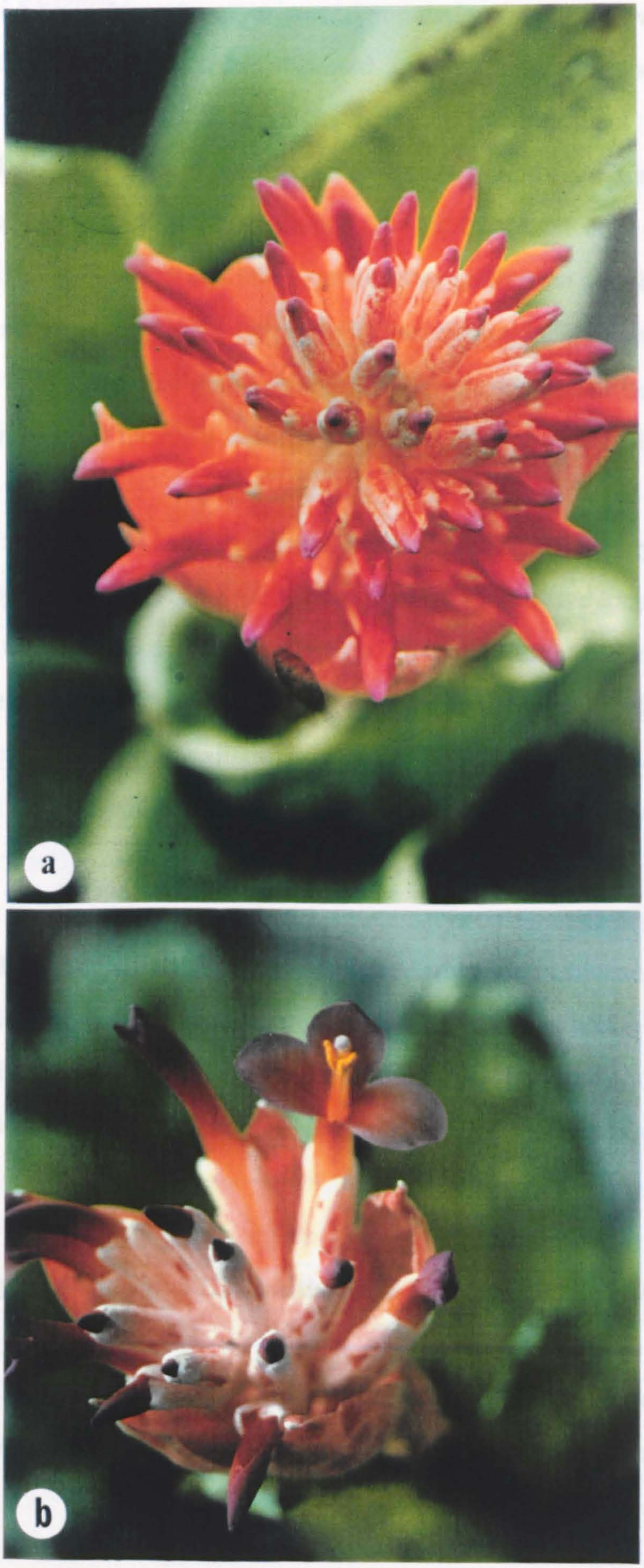
POLLINATION BIOLOGY: Anthesis of Billbergia pyramidallis var. pyramidallis showed that when the flowers opened the anthers were releasing pollen and the stigma was apparently receptive, with no distinguishable dichogamy.

The septal nectary releases the nectar by three pores located on the floor of hypanthium and the petal appendages are fimbriate, partitioning the intrafloral chamber in a lower chamber and forming a capillary space delimited by the inner hypanthium floor, wall, and petal appendages.

The volume and sugar concentration of nectar (Table 5) were measured in flowers in which the complete inflorescence was previously bagged. The maximum volume of nectar in a single flower was 32.8μl (N=1) and the mean concentration of sucrose equivalents was 32% (N=8, SD±3.55, range 20-37%).

The bright rose primary bracts and red and blue corolla seems to be the principal advertisement for the pollinator. The visitor to this species in the study area of Macaé de Cima Ecological Reserve, Nova Friburgo, was the hummingbird Phaetornis eurynome, and in the Araras, Petrópolis was another hummingbird, Melanotrochillus fuscus, both birds touching the stigma during their visits.

Plate 5.19. (a) inflorescence and (b) flower of *B. pyramidallis* var. *pyramidallis*.


a
b

BREEDING SYSTEM: An experimental population was created with a sample of three individuals which were collected in both natural populations and cultivated in the glasshouse of the Plant Sciences Laboratory of St. Andrews University. Two individuals flowered, in different periods, limiting the hand-pollination experiments to self-pollinations (N=16) treatment only. Eight selfed pistils were fixed at 24, 48, 72 and 96h intervals after pollination and the remainder were left to set fruit. Billbergia pyramidallis var. pyramidallis seems to be self-incompatible with self-pollen grains germinating on the stigma but failing to grow into the ovary. None of the eight selfed pistils left on the plants set fruits.

SUMMARY: This species exhibited 'cornucopia' flowering phenology, during the month of September at Macaé de Cima Ecological Reserve population and December in the population of Araras, Petrópolis. It has diurnal flowering and was visited by the hummingbirds Phaetornis eurynome and Melanotrochillus fuscus. Billbergia pyramidallis var. pyramidallis seems to be self-incompatible although a larger sample of hand-pollinations of individuals and flowers would be needed to confirm this.

BOTANICAL SPECIMENS: Rio de Janeiro State: Macaé de Cima Ecological Reserve, Nova Friburgo, 20/IX/1992, G.Martinelli 14689 (RB; cultivated RB, University of St. Andrews); Araras, Petrópolis, 2/XII/1992, G.Martinelli 14696 (RB; cultivated RB, University of St. Andrews).

5.19. Dyckia pseudococcinea L.B.Smith [Table 5; Figure 5; Plate 5.20,a,b]

MORPHOLOGY: Plant to 1.60m high when flowering. Inflorescence simple or rarely with a small branches at the base and with floral bracts orange. Sepals and petals orange, stamens with the filaments connate for 2mm above the common tube with the petals, style very short, stigma conduplicate spiral. Fruit capsule.

DISTRIBUTION AND HABITAT: Terrestrial, in sandy soils of restingas, or saxicolous plants in maritime outcrops, in the Atlantic Rainforest province, near the sea level. From Rio de Janeiro to Paraná. The species was studied in Paraty, Paratymirim, where occurs as saxicolous in maritime outcrops at sea level.

FLOWERING PHENOLOGY: The flowering period of Dyckia pseudococcinea occurred between September and October in the study area (Figure 5), with no defined peak of flowering. The phenological pattern was determined as 'steady state'. Fruiting occurred in November and early-December. The mean number of flowers per inflorescence was 55 (N=4), with the first flowers to open at the base of the inflorescence such that flowering occurs in a ascending sequence.

POLLINATION BIOLOGY: The inflorescence of this species was almost always frequented by ants which fed on the nectar secretion that escaped from the flowers, since Dyckia pseudococcinea does not have petal appendages to maintain the nectar within the corolla, and the flowers are slightly directed downward.

Diurnal visitors to the flowers of this species were a unidentified bumble bee, and a butterfly (Hesperiidae). However, the hummingbird Amazilia fimbriata was also observed to visit flowers of this species sporadically and it is likely that D. pseudococcinea is most likely pollinated by hummingbirds.

The sugar concentration of Dyckia pseudococcinea (Table 5) was measured in flowers previously bagged. The mean of concentration of sucrose equivalents was 29% (N=6, SD±4.06, range 24-35%).

BREEDING SYSTEM: An experimental population was created with a sample of three individuals which were collected in the early stage of flowering from two different natural populations and cultivated in Araras, Petrópolis. Experimental hand-pollinations were performed with previously bagged flowers (N = 17), and a sample of hand-pollinated pistils from different treatments were fixed at 96 hours after pollination and the natural fruit-set observed from tagged flowers of the natural population showed a low percentage of fruit-set: 43.7% (7/16). This species seems to be self-compatible, with sequence of both self- and cross-pollinated pistils showing that the pollen grains germinated on the stigma and in 96 hours the ovule penetration was high in selfed pistils (CP: mean = 19.5%, N = 7, range 2.3-34.4%; SP: mean = 70.9%, N = 10, range 59.8-83.3%; $P > 0.01$).

SUMMARY: Dyckia pseudococcinea exhibits 'steady state' flowering phenology, during the months of September and October in the study area. It has diurnal flowers, and is visited by hummingbirds and butterflies, and appears to be self-compatible.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 11/X/1992, G.Martinelli 14739 (RB).

5.20. Neoregelia compacta (Mez) L.B.Smith [Tables 5; Figure 5]

MORPHOLOGY: Plant saxicolous, terrestrial or epiphytic, with the leaves forming a dense rosette, and when in flowering the inner leaves of rosette reddish. Inflorescence sunk in the rosette, with flowers with pale red petals, the stamens included.

DISTRIBUTION AND HABITAT: Endemic to Rio de Janeiro State, occurring as epiphytic, saxicolous or terrestrial in maritime outcrops, 'restingas' and lowland wet forests of the Atlantic Rainforest province at sea level. The species was studied in Paraty, Paratymirim, Rio de Janeiro.

FLOWERING PHENOLOGY: The flowering period of Neoregelia compacta occurred in October and November and the fruiting occurred in January, in the study area.

POLLINATION BIOLOGY: As with N.marmorata (see below) it was difficult to gain access to the small and partially submersed flowers of this species, and observations on the floral biology and anthesis development were not realized. The inflorescence is deep in the centre of the rosette and partially covered by the rain-water accumulated into the funnelform rosette. In the majority of the plants monitored in the study area, the base of the flowers were submersed in the water-tank, such that the mouth of the corolla at the level of the water, and the imbricate petals prevent the water from entering the floral tube. During very heavy rains, however, it was also observed that the flowers became completely submersed in the 'water-tanks' for a short period of time.

As the corolla opened, the anthers were releasing pollen and the stigma, apparently receptive, was located between the anthers. Almost all flowers observed in plants of natural population had pollen grains on the stigma just prior to flower opening.

The bright red of inner leaves of the rosette and the rose petals seem to be the principal advertisement for the pollinator. The volume and concentration of nectar was not measured in this species.

Visitors to Neoregelia compacta were the hummingbirds Chlorostilbon aureoventris and Amazilia fimbriata, both touching the stigma and the anthers during their visits, and they presented a defined routine and frequency in their visits to flowers of this species.

BREEDING SYSTEM: No experiments of hand-pollination were made due the difficult morphology and difficult access to the small sized flowers.

SUMMARY: Neoregelia compacta flowered during October and November in the study area. It has diurnal-flowering, and seems to be pollinated by the hummingbirds Chlorostilbon aureoventris and Amazilia fimbriata.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 21/XI/1992, G.Martinelli 14720 (RB, cultivated RB, E).

5.21. Neoregelia marmorata (Baker) L.B.Smith [Tables 5; Figure 5; Plate 5.20c]

MORPHOLOGY: Plant terrestrial or saxicolous with the leaves yellowish red with red spotts forming a densely funnelform rosette. Inflorescence sunk in the centre of rosette. Flowers with green sepals and white petals turning pale rose during the anthesis. Stamens markedly included.

DISTRIBUTION AND HABITAT: This species occurs as saxicolous or terrestrial plant on maritime outcrops, coastal thickets, mangroves and lowland wet forests at sea level, in the southeastern section of the Atlantic Rainforest province, in the Rio de Janeiro and São Paulo States. It was studied in Paraty, Paratymirim, at sea level.

FLOWERING PHENOLOGY: The flowering period of Neoregelia marmorata began in January and finished in February in the study area and the fruiting occurred in April (Figure 5). This species opened 1-4 flowers per day and seems to be day-blooming, with the anthesis beginning around 06:00h.

Plate 5.20. (a) butterfly (Hasperiidae) visiting flowers of Dyckia pseudococcinea; (b) habit of D. pseudococcinea; (c) inflorescence in the interior of rosette of Neoregelia marmorata.


a
b
c

POLLINATION BIOLOGY: Due the difficulties of access to the small flowers of this species, in which the inflorescence is deep in the centre of rosette and partially covered by the rain-water accumulated in the crateriform rosette, the observations on floral biology and anthesis development were not realized. In almost all individuals observed in the population, the base of the flower was submersed in the water-tank formed by the leaves, such as the the mouth of the corolla is at the level of the water, and the imbricated petals prevent the water from filling the floral tube.

When the flowers open the stamens are releasing pollen and the stigma is apparently receptive, with no evident dichogamy. Flowers of some individuals were observed with pollen on the stigma just prior the corolla aperture. The petals change colour during the anthesis from pale-rose to white color.

The yellowish-green with red-spotted leaves, and the pale-rose petals, seem to be the main advertisement for the pollinator.

The volume and sugar concentration of nectar (Table 5) was measured in flowers in which the plants was previously wholly bagged. The mean of concentration of sucrose equivalents was 26% (N=4, SD±1.03, range 24-30%), and the volume of nectar in a single flower was 17.9μl (N=1).

The principal visitor to Neoregelia marmorata in the study area was the hummingbird Chlorostilbon aureoventris, which hovered over the inflorescence and with the head and beak down directed downwards and sucked the nectar of the flowers, touching the stigma and anthers with the beak. This hummingbird was not frequent in its visits to the flowers, but it did present a regular sequence of visits to individual plants and flowers.

BREEDING SYSTEM: No hand-pollinations experiment were made due the small size and difficult access to the flowers.

SUMMARY: The flowering of Neoregelia marmorata was in January and February. It has a diurnal anthesis, and seems to be pollinated by the hummingbird Chlorostilbon aureoventris.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 05/II/1992, G.Martinelli 14783 (RB; cultivated RB, E).

5.22. Nidularium billbergioides (Schultes f.) L.B.Smith var. billbergioides

[Table 5; Figure 5; Plate 5.21a]

MORPHOLOGY: Plant propagating by long ascending rhizomes, and with the leaves forming a funnelform rosette. Inflorescence compound and few-flowered, primary bracts orange or sometimes brownish-red. Flowers with petals white and connate for 2/3 of the length.

DISTRIBUTION AND HABITAT: This species occurs as epiphytic or terrestrial plant in lowland wet forest from sea level to 400m of altitude, in the southeastern sector of the Atlantic Rainforest province in the Rio de Janeiro and São Paulo States. The species was studied at Paraty, at sea level.

FLOWERING PHENOLOGY: The flowering period of Nidularium billbergioides var. billbergioides began in November and finished in December in the study area. Fruiting occurred between January and February.

POLLINATION BIOLOGY: N.billbergioides var. billbergioides was visited by the hummingbird Chlorostilbon aureoventris in the study area. The orange or brownish-red colour of the primary bracts and white petals, seem to be the principal advertisement for the pollinator. The volume and sugar concentration of nectar was not measured in this species.

BREEDING SYSTEM: No experiments on breeding system were carried out due their size and difficult access to the flowers.

SUMMARY: Nidularium billbergioides var. billbergioides seems to be a hummingbird pollinated species with a flowering period between November and December.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 29/XI/1992, G.Martinelli 14799 (RB).

5.23. Nidularium scheremetiewii Regel [Tables 5; Figure 5; Plate 5.21b]

MORPHOLOGY: Plant to 50cm high when flowering, with the leaves forming a dense rosette. Inflorescence few-flowered, with primary bracts bright red. Flowers with the petals highly connate, dark blue with margins and base white; stamens included.

DISTRIBUTION AND HABITAT: Terrestrial and epiphytic plants in lowland and montane wet forest of the Atlantic Rainforest province, between 500-1000 m of altitude, ranging from Espírito Santo State to Santa Catarina State. The species was studied in Macaé de Cima Ecological Reserve, Nova Friburgo, Rio de Janeiro State, at 1000 m of altitude.

FLOWERING PHENOLOGY: The period of flowering of Nidularium scheremetiewii began in mid-February and finished in early-March. The fruiting

Plate 5.21. (a) inflorescence and flowers of Nidularium billbergioides var. billbergioides; (b) inflorescence and flowers of Nidularium scheremetiewii.


a
b

occurred between March and April in the study area (Figure 5). This species presented diurnal flowers with the anthesis beginning around 6:30h.

POLLINATION BIOLOGY: The principal visitor of Nidularium scheremetiewii was the hummingbird Heliothryx aurita which visited frequently the flowers of this species. The bright red primary bracts and the dark blue corolla seems to be the principal advertisement for the pollinator.

The mean nectar concentration of sucrose equivalents of this species was 27% (N=4, SD±3.12, range 19-30%).

BREEDING SYSTEM: No hand-pollination experiments were made with this species due the difficult access to the flowers.

SUMMARY:Nidularium scheremetiewii flowered between February and March and was visited by the hummingbird Heliothryx aurita in the study area.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Macaé de Cima Ecological Reserve, Nova Friburgo, 01/II/1993, G.Martinelli 14787 (RB).

5.24. Quesnelia augusto-coburgii Wawra [Table 5; Figure 5; Plate 5.22a]

MORPHOLOGY: Plant propagating by erect basal rhizomes, 1.30m high when flowering. Leaves few, forming a cylindrical rosette. Inflorescence with yellow-green floral bracts and flowers with red sepals and purple petals, the latter recurved at the apex and exposing the anthers and stigma at anthesis. Each petal with bearing two fimbriate appendages at base; stigma conduplicate-spiral.

DISTRIBUTION AND HABITAT: Epiphytic or saxicolous plants in montane wet forests of the Atlantic Rainforest province, at 400-1100m of altitude, occurring in the Rio de Janeiro and Minas Gerais States. The species was studied in Araras, Petrópolis, at 1100m of altitude, Rio de Janeiro State, where it occurs as a saxicole.

FLOWERING PHENOLOGY: Quesnelia augusto-coburgii the flowering during August-September (Figure 5), with a 'cornucopia' phenological type. Fruiting occurred in early-October to mid-March. This species had diurnal flowers with the anthesis beginning c. 06:00h.

POLLINATION BIOLOGY: Shortly after the flower of this species open, the petals become recurved, exposing the anthers. The stigma is located c. 3-4mm above the anthers so that approach herkogamy is indicated, but dichogamy was not observed in this species. The first flowers to open were those of the base of the inflorescence such that the flowering occurs in a ascending sequence. The mean number of flowers per inflorescence was 16 (N=18).

The inflorescence is very attractive and the red or rose coloured floral bracts, yellowish-green axis, and purple petals, seem to be the principal advertisement for the pollinators. The petals change the colour at the end of anthesis, from purple to red.

The septal nectary releases the nectar by three pores located on the floor of hypanthium. The petal appendages are fimbriate, partitioning the intrafloral chamber in a lower chamber forming a capillary space delimited by the inner hypanthium floor, wall, and the petal appendages. The mean concentration of sucrose equivalents of nectar of Quesnelia augusto-coburgii was 25% (N=8, SD ± 1.02, range 21-29%). The nectar was available when the flower opened.

Visitors to this species in the study area were the hummingbirds Phaetornis petrei and Leucochloris albicollis. The former visited regularly and frequently whilst Leucochloris albicollis was sporadic in its visits. Both species of hummingbirds made contact with the stigma whilst foraging for nectar at the flowers.

BREEDING SYSTEM: Although several hand-pollination experiments were made into this species, including self- and cross-pollination treatments, no pistils were encountered with penetrated ovules due to a fungal contamination of the stigmas. A natural fruit-set of 60% (18/30) was obtained in tagged flowers of natural population.

SUMMARY: Quesnelia augusto-coburgii exhibits 'cornucopia' flowering phenology, during August-September. It has diurnal flowers and seem to be pollinated by the hummingbirds Phaetornis petrei and Leucochloris albicollis, in the study area.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Araras, Petrópolis, 14/IX/1992, G.Martinelli 14697 (RB; cultivated RB, E).

5.25. Quesnelia liboniana (De Jonghe) Mez [Table 5; Figure 5; Plate 5.22b]

MORPHOLOGY: Plant propagating by rhizomes; leaves few, forming a cylindrical rosette. Inflorescence simple or sometimes with a small 1-2 flowered branch at base, and with red floral bracts. Flowers with red sepals and petals dark blue, with their apices slightly recurved at anthesis. Each petal bearing two fimbriate appendages at base; filaments of the second series of stames half adnate to the petals; stigma conduplicate-spiral.

DISTRIBUTION AND HABITAT: This species occurs as epiphytic plant, endemic in montane wet forest in the southeastern sector of the Atlantic Rainforest province, between 700-1200m of altitude, in Rio de Janeiro State. The species was studied in Macaé de Cima Ecological Reserve, Nova Friburgo, Rio de Janeiro State, at 1100m of altitude.

FLOWERING PHENOLOGY: The flowering period of Quesnelia liboniana began in October and finished in early November Fruiting ocurred in December (Figure 5). The flowers are diurnal with the anthesis beginning c. 06:30h.

POLLINATION BIOLOGY: The principal advertisement for pollinators in this species appears to be the bright red inflorescence and the dark blue corolla. The volume and sugar concentration of nectar of Quesnelia liboniana was not measured.

The principal visitors of this species in the study area, were the hummingbirds Phaetornis sp. and Clitolaema rubricauda, both of which visited the flowers periodically.

BREEDING SYSTEM: No hand-pollination experiments were made in this species.

SUMMARY: The flowering period of Quesnelia liboniana was in October and November in the study area. It has a diurnal anthesis and is visited by the hummingbirds Phaetornis sp. and Clitolaema rubricauda.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Nova Friburgo, Macaé de Cima Ecological Reserve, 28/IX/1986, G.Martinelli 11719 & al. (RB); idem, 20/XI/1992, G.Martinelli 14733 (RB); idem, 14/X/1992, G.Martinelli 14797 (RB; cultivated RB).

5.26. Quesnelia marmorata (Lemaire) R.W.Read [Table 5; Figure 5]

MORPHOLOGY: Plant propagating by short rhizomes, 60cm high when flowering, with the leaves forming a cylindrical rosette. Inflorescence with slightly decurved scape and primary bracts bright rose. Flowers with purple sepals and blue petals, each petal bearing two appendages at base; stamens included.

DISTRIBUTION AND HABITAT: This species occurs as an epiphytic plant in mangroves, restinga, and lowland and montane wet forest of the Atlantic Rainforest province, from sea level to 1000m of altitude. The species was studied in Paraty, Paratymirim, Rio de Janeiro State, where occurs as epiphytic, at sea level.

FLOWERING PHENOLOGY: The flowering period of Quesnelia marmorata began in November and finished in December in the study area. Fruiting occurred in January. (Figure 5). The flowers opens c. 06:00h.

POLLINATION BIOLOGY: At the time of the flowers opened, the anthers were releasing pollen, and the stigma was apparently receptive, with no aparent dichogamy. The anthesis began c. 06:00h and finished c. 8 hours later. The petals change from blue to red colour during this period.

The bright rose floral bracts and blue corolla seems to be the principal advertisement for the pollinator.

The volume and sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The maximum volume of nectar in a single flower was 27.9μl (N = 1) and the mean of concentration of sucrose equivalents was 28% (N = 4, SD ± 1.03, range 24-30%).

The only visitor of Quesnelia marmorata in the study area was an unindentified hummingbird, which visited sporadically the flowers of the monitored individuals.

BREEDING SYSTEM: An experimental population was created throughout a sample of three individuals which were collected in the natural population and cultivated in the glasshouse of the University of St. Andrews. Only one individual has flowered, limiting the hand-pollination experiments to a self-pollination treatment only. Selfed pistils were fixed in 72 and 96 hours after pollination.

Quesnelia marmorata seems to be self-incompatible (Table 5), since although the self-pollen grains germinated on the stigma, they did not develop pollen tubes in the style. A large number of hand-pollinations would be necessary to confirm this.

SUMMARY: This species exhibits 'cornucopia' flowering phenology type, during November-December. It has a diurnal flowers visited by hummingbirds, and appears to be self-incompatible, with the site of self-incompatibility located in the stigmatic head.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 26/XI/1992, G.Martinelli 14719 (RB; cultivated RB, E, University of St.Andrews).

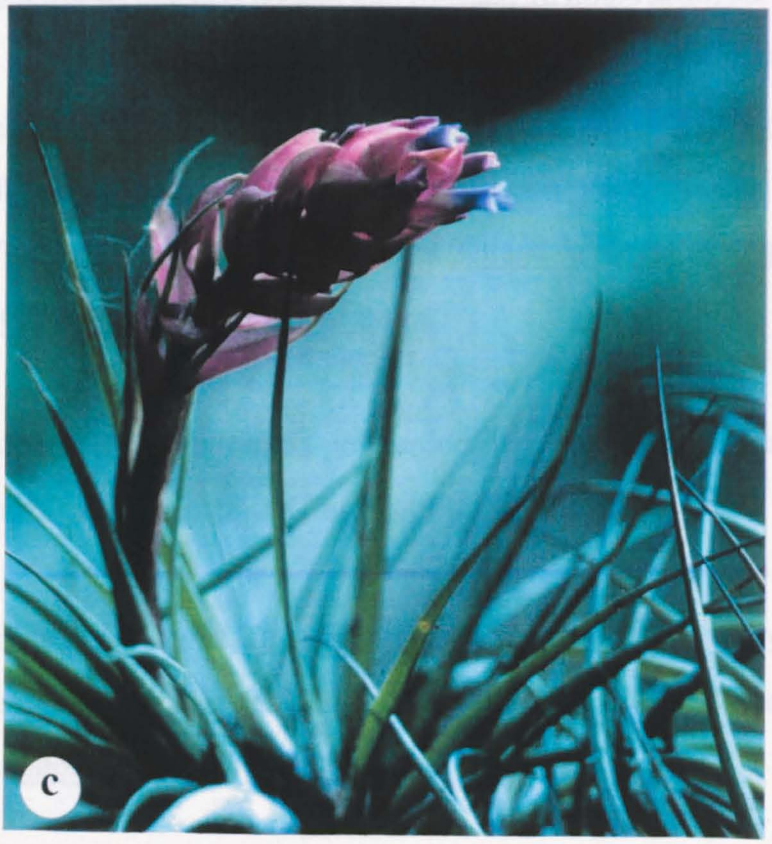
5.27. Tillandsia stricta Solander var. stricta [Table 5; Figure 5; Plate 5.22c]

MORPHOLOGY: Plant to 22cm high when flowering. Inflorescence simple with the floral bracts yellowish white to red, with the lower most bracts exceeding the flowers. Flowers with petals purple, stamens included with the filaments plicate.

Plate 5.22. (a) flowers of Quesnelia augusto-coburgii; (b) inflorescence of Quesnelia liboniana; (c) inflorescence and flowers of Tillandsia stricta var. stricta.


a


b


c

DISTRIBUTION AND HABITAT: This species presents a large geographical distribution, from Venezuela to Argentina. In Brazil it occurs as epiphyte in gallery forest, and as a saxicole in open rocky-savannas ('campos rupestres') in Minas Gerais, and on granitic outcrops in restingas, mangroves, lowland and wet forests, and high montane grassland in the Atlantic Rainforest province, from sea level to 1900m of altitude. The species was studied in Paraty, Paratymirim.

FLOWERING PHENOLOGY: The flowering period of Tillandsia stricta var. stricta began in August and finished in early-September in the study area. Fruiting occurred in early-October. This species open 2-4 diurnal flowers per day and presented 'cornucopia' phenological type.

POLLINATION BIOLOGY: The yellowish white and sometimes red floral bracts, and the purple petals appear to be the principal advertisement for the pollinator. The anthesis began c. 05:00h and finished 10 hours after. At the time the flower opens, the anthers were releasing pollen and the stigma was apparently receptive. The petals change the colours from purple in the beginning of anthesis, to red, and yellowish white to the end of anthesis.

The only visitor to the flowers of Tillandsia stricta var. stricta was the hummingbird Chlorostilbon aureoventris.

BREEDING SYSTEM: No hand-pollination experiments were made, due the small size and difficult access to the flowers of this species.

SUMMARY: The flowering of Tillandsia stricta var. stricta in the study area was in August and early September. It has diurnal anthesis, and was visited by the hummingbird Chlorostilbon aureoventris.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, 12/VIII/1992, G.Martinelli 14800 (RB).

5.28. Vriesea altomacaensis Costa [Table 5; Figure 5; Plate 5.23a]

MORPHOLOGY: Plant to 1.50m high when flowering and with the leaves forming a dense funnelform rosette. Inflorescence bipinnate, with floral bracts yellowish-green. Flowers distichous, becoming partially secund at anthesis, with yellow sepals and with petals yellowish green with green apex, each petal bearing two appendages; stamens included, stigma exserted.

DISTRIBUTION AND HABITAT: This species is narrow endemic to the Macaé de Cima Ecological Reserve, Nova Friburgo, Rio de Janeiro State, where occurs as a terrestrial plant in montane wet forest ('mist forest'), at 1300-1400m of altitude.

FLOWERING PHENOLOGY: The flowering period of Vriesea altomacaensis began in December and finished in January in the study area (Figure 5). Fruiting occured in February and March.

POLLINATION BIOLOGY: The diurnal anthesis of Vriesea altomacaensis showed dichogamy with a clear protandry. In the early hours of the anthesis, the stigma is not receptive and is located c. 4mm above the apex of the anthers and gradually extends to reach 8-9mm beyond the anthers, when it became to be receptive. The spatial separation of the anthers and stigma was classified as approach herkogamy. The yellow color of the floral bracts and flowers seems to be the advertisement for the pollinator.

The sugar concentration of nectar of this species (Table 5) was measured in previously bagged flowers. The mean concentration of sucrose equivalents was 24% (N=4, SD ± 1.61, range 24-26%).

The principal visitors to Vriesea altomacaensis were the hummingbirds Stephanoxis lalandi, Clytolaema rubricauda and Leucochloris albicollis. The hummingbird Stephanoxix lalandi seemed to be the most effective vector of this group due its frequency in the study area, and the fact that it always touched the stigma during the visits. Other visitors observed were small wild bees, which landed on the flowers without touching the stigma.

BREEDING SYSTEM: Due to the rarity of this endemic species no specimens were taken into cultivation and no hand-pollination experiments were realized. The natural fruit-set of 64% (31/50) was obtained from tagged flowers of natural population.

SUMMARY: Vriesea altomacaensis flowered during the months of December and January. It has a diurnal flowering and seems to be pollinated by the hummingbirds Stephanoxis lalandi, Clitolaema rubricauda and Leucochloris albicollis.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Macaé de Cima Ecological Reserve, Nova Friburgo, 28/XII/1993, G.Martinelli 14713 (RB, cultivated RB, E).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Macaé de Cima Ecological Reserve, Nova Friburgo, 28/XII/1993, G.Martinelli 225-ZOO: 'small bees' unindentified (St.Andrews Univ.); idem, 29/XII/1993, G.Martinelli 226-ZOO: Stephanoxis lalandi (R).

5.29. Vriesea atra Mez var. atra [Table 5; Figure 5]

MORPHOLOGY: Plant with 1.80m high when flowering; leaves forming a dense funnelform rosette. Inflorescence simple, to 80cm long, with the floral bracts dark chestnut with green margins and red-spotted. Flowers distichous with pale-brown and coriaceous sepals, and petals initially yellow, and them white from the middle to the end of the anthesis. Each petal bearing two large appendages at base.

DISTRIBUTUTION AND HABITAT: This endemic species occurs as saxicolous plants on the high montane grassland of Rio de Janeiro State, southeastern section of the Atlantic Rainforest province, between 1500-1800m of altitude. The species was studied in Araras, Petropolis, at 1600m of altitude.

FLOWERING PHENOLOGY: The flowering period of Vriesea atra var. atra began in October and finished in December in the study area. The fruiting occurred in January and February (Figure 5). This species opens one to two flowers late afternoon and is night-blooming, with the anthesis beginning around 17:30h.

POLLINATION BIOLOGY: The development of the anthesis of Vriesea atra var. atra showed a slight protandry, with the stigma, in the early hours of anthesis, not receptive. The stigma developed from being initially at the same height as the anthers, to 3 mm above some 3-4 hours later, when it become to be receptive.

The white petals and the faint smell of the flowers, seem to be the most important attractive advertisement for the pollinator.

The volume and sugar concentration of nectar (Table 5a.1) was measured in previously bagged flowers. The maximum volume of nectar in a single flower was 209μl (N = 1) and the mean of concentration of sucrose equivalents of 13% (N = 6, SD ± 3.74, range 9-19%).

The visitors of Vriesea atra var. atra were the bats Anoura caudifer and other unindentified species. One specimen of Anoura caudifer which was captured in mist nets near the population showed pollen grains of Bromeliaceae on the snout and forehead.

BREEDING SYSTEM: Due the difficulties of access to the rocky faces of the mountains where this species occurs, only two plants from the same cluster were obtained to cultivate and hand-pollinations were limited to self-pollination treatments (N = 6). All self-pollinated pistils were fixed at intervals of 72 and 96 hours after pollination.

This species is most likely to be self-compatible since the self-pollen grains germinated on the stigma and a mass of pollen tubes could be distinguished in the style.

By 72h post-pollination self-pollen tubes had reached the ovary, with no ovule penetration, whilst at 96h ovule penetration were 68.6% (N = 3, range 65.2-71.2%).

SUMMARY: Vriesea atra var. atra exhibits 'steady state' flowering phenology, during the months from October to early December. It has a nocturnal flowering, and is pollinated by the small bat Anoura caudifer in the study area. The partial data on the breeding system suggest that this species appear to be self-compatible.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Araras, Petrópolis, 21/IX/1980, G.Martinelli 7387 (RB); idem, 04/XII/1992, G.Martinelli 14703 (RB).

ZOOLOGICAL SPECIMENS: Rio de Janeiro State: Araras, Petrópolis, 22/XII/1992, G.Martinelli 224-ZOO: Anoura caudifer (RioZoo).

5.30. Vriesea flammea L.B.Smith [Table 5; Figure 5]

MORPHOLOGY: Plant c. 50cm when flowering, also propagating asexualy by slender rhizomes. Leaves dark green or sometimes chestnut and violet-spotted. Inflorescence small, 11cm long with floral bracts bright red. Flowers with white petals, each petal bearing a small appendage at the base of the petal, and with stamens and pistils exserted.

DISTRIBUTION AND HABITAT: This species occurs as epiphytic or saxicolous plants in the lowland wet forest of the Atlantic Rainforest province, maritime outcrops and mangroves, with an altitudinal range between the sea level to 500m of altitude, and from Rio de Janeiro to Santa Catarina State. The species was studied in Paraty, Paratymirim, in lowland wet forest at sea level.

FLOWERING PHENOLOGY: The flowering period of Vriesea flammea extended from November to early December, with a definite peak of flowering in November in the study area. The fruiting period is between January and February. This species opened one flower per day, with diurnal blooming, with flowers beginning to open c. 06:00h. Flower phenology is thus of the 'steady state' type.

POLLINATION BIOLOGY: Flowers of Vriesea flammea showed dichogamy with a slight protandry, such that in the early hours of the anthesis, the stigma was not receptive and was located at the same height as the apex of the anthers, and gradually extended to reach 3mm above the apex of the anthers.

The bright red of the floral bracts and the petals white seems to be the advertisement for the pollinator. The septal nectaries have three slits in the gynoecial suture. The petal appendages embrace the base of the style, partitioning off the intrafloral chamber with a lower compartment, where the nectar is released.

The volume and sugar concentration of nectar of this species were not measured. The only visitor observed visiting the flowers of Vriesea flammea was the hummingbird Clitolaema rubricauda, which did not present a defined pattern of frequency or routine in its visits.

BREEDING SYSTEM: No experimental hand-pollinations were made with this species due to the low number of flowers available. The results of natural fruit-set was obtained from previously tagged flowers, in 4 individuals of the natural population of the study area was 63.6% (7/11).

SUMMARY: Vriesea flammea flowered during the months of November and December and had a diurnal flowers, and was visited by the hummingbird Clitolaema rubricauda in the study area.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Paraty, Paratymirim, Ilha da Cotia, 28/XII/1992, G.Martinelli 14659 (RB; cultivated RB, E).

5.31. Vriesea haematina L.B.Smith [Table 5; Figure 5; Plate 5.23b,c,d]

MORPHOLOGY: Plant when flowering to 1m high with the leaves forming a funnelform rosette. Inflorescence compound, red, with the floral bracts red with yellow margins. Flowers with yellow petals, each petal bearing two appendages at base.

DISTRIBUTION AND HABITAT: This species is endemic to the montane wet forest of the southeastern sector of the Atlantic Rainforest province in the State of Rio de Janeiro, between 1000-1200 m of altitude, where occurs as epiphytes in small populations. The species was studied in the Ecological Reserve of Macaé de Cima , Nova Friburgo, at 1000 m of altitude.

FLOWERING PHENOLOGY: The flowering period of Vriesea haematina began in December and finished in February in the study area (Figure 5). Fruiting occurred in March. This species opened c. 2-4 flowers per day, and the mean number of flowers per inflorescence was 112 flowers (N=3). Plants is thus of the 'steady state' flowering phenology type. The species has diurnal flowering, with the flowers open at c. 06:30h.

POLLINATION BIOLOGY: Flowers of Vriesea haematina showed dichogamy with a slight protandry. In the early hours of the anthesis, the stigma was not receptive and has located at the same height of the middle of the anthers, but with styles elongation it reaches c. 3-4mm above the apex of the anthers. The red inflorescence, with floral bracts red and yellow, and the petals yellow seem to be the attractive advertisement for the pollinator.

The septal nectaries have three slits in the gynoecial suture. The petal appendages embrace the base of the style, partitioning the intrafloral chamber into a lower compartment, where the nectar is released.

The volume and sugar concentration of nectar (Table 5a.1) was measured in previously bagged flowers. The volume of nectar in a single flower was 137μl (N=1) and the mean of concentration of sucrose equivalents was 21% (N=10, SD±1.47, range 19-23%).

The principal visitors to this species were the hummingbirds Leucochloris albicollis, Stephanoxis lalandi, and Clitolaema rubricauda. The hummingbird Leucochloris albicollis and Stephanoxis lalandi were the most frequent visitors of flowers of this species, both birds touched the stigma and the anthers during their visits.

BREEDING SYSTEM: An experimental population of Vriesea haematina was created with just 2 individuals which were collected from the natural population. Since these plants did not flower at the same period of time, only self-pollinations were possible. The pistils from some self-pollinations were fixed at 72 hours. Fruit-set from other self-pollinated flowers was followed until maturation, and the natural fruit-set was monitored with tagged flowers on three differents plants in the population.

The self-pollinated pistils showed that the pollen grains germinated on the stigma and pollen tubes could be distinguished in the style, with 74.6% of the ovules penetrated at 72 hours after pollination (N=6, range 61.2-96.2%). The fruit-set from selfed pistils was 44.4% (4/9) and the natural fruit-set was 64.3% (9/14).

SUMMARY: Vriesea haematina exhibits 'steady state' flowering phenology, during the months of December, January and February. It has a diurnal flowering, and was pollinated by the hummingbirds Leucocloris albicollis and Stephanoxis lalandi. The species seems to be self-compatible although a large sample/number of hand pollinations would be needed to confirm this.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Nova Friburgo, Macaé de Cima Ecological Reserve, 20/XII/1992, G.Martinelli 14689 (RB, cultivated RB, E).

Plate 5.23. (a) inflorescence of Vriesea altomacaensis; (b) inflorescence of Vriesea haematina; (c) flower of V. haematina; (d) the hummingbird Stephanoxis lalandi, pollinator of V. haematina.


a
b
c
d

5.32. Vriesea longicaulis (Baker) Mez [Table 5; Figure 5]

MORPHOLOGY: Plant with 1.40m high when flowering, with leaves forming a funnelform rosette. Inflorescence simple or rarely with a small branch at base and with the floral bracts pale brown. Flowers secund at anthesis with the calyx hidden by the floral bracts and petals yellow with brown margins, each petal bearing two large appendages at base; stamens included.

DISTRIBUTION AND HABITAT: This species occurs as epiphytic or terrestrial plants in the montane wet forest, between 800-1900 m of altitude ranging from the southeastern to south sector of the Atlantic Rainforest province. The species was studied in Fazenda Ingleza, Petrópolis, Rio de Janeiro State, as terrestrial in "mist forest", at 1300m of altitude.

FLOWERING PHENOLOGY: The flowering period of Vriesea longicaulis in the study area was from December to early February. Fruiting occurred in March and April (Figure 5). This species seems to be night-blooming, opening one, rarely two flowers per night, with anthesis beginning c. 16:30h. The mean number of flowers per plant was 22 (N=2).

POLLINATION BIOLOGY: Anthesis in Vriesea longicaulis showed dichogamy with a well defined protandry. In the early hours of the anthesis, the stigma is not receptive and is located c. 1mm above the apex of the anthers, and it gradually extended to reach 4mm above the anthers, by which time it was receptive. The yellow corolla with the brown margins of the petals and the slight odour of the flower during the anthesis, seem to be the important advertisement for the pollinator.

The sugar concentration of nectar was measured in previously bagged flowers. The mean of concentration of sucrose equivalents was 17% (N=4, SD±2.12, range 16-20%).

No observations on the visitors and pollinators were made. Most likely this species is pollinated by small bats or nocturnal hawkmoths, as previously suggested by Vogel (1969).

BREEDING SYSTEM: Only two plants of this species were encountered in flower, so that hand-pollination experiments were very limited. Self-pollinations were performed with previously bagged flowers (N=7) and selfed-pistils were fixed at 48 and 72 hours after anthesis. The fruit-set from hand-pollinated flowers and from the natural population were not obtained.

This species seems to be self-compatible since the self-pollen grains germinated on the stigma and pollens tubes could be distinguished in the style, and penetrated the ovules by 48 hours (62.1%, N=2, range 61.1-63.2%). At 72 hours the percentage of penetrated ovules was 75.8% (N=5, range 69.1-79.4%).

SUMMARY: Vriesea longicaulis flowers during the months of December to January. It has a nocturnal flowering, and is most likely to be pollinated by small bats or nocturnal hawkmoths. The preliminary data on the breeding system of this species suggests that it is self-compatible.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Petrópolis, Fazenda Inglesa, 04/II/1993, G.Martinelli 14693 (RB, cultivated RB, E).

5.33. Vriesea paraibica Wawra [Table 5; Figure 5; Plate 5.24a,b,c]

MORPHOLOGY: Plant epiphytic with 30cm high when flowering, and with leaves forming a funnelform rosette. Inflorescence simple with floral bracts red with green apex; sepals yellow and petals yellow. Each petal bearing two lanceolate appendages at base; the stamens and the stigma are exserted.

DISTRIBUTION AND HABITAT: This rare species is endemic to the montane wet forest of southeastern sector of the Atlantic Rainforest province, between 1000 - 1200 m of altitude, where it occurs as epiphytes with rather isolated individuals in small populations. The species is typified by original description and plate, and was only recently rediscovered in the study area.

FLOWERING PHENOLOGY: The flowering period of Vriesea paraibica began in early January and finished in February in the area of study. The fruiting occurred in March (Figure 5). This species opens one to two flowers per day with a mean number of flowers per inflorescence of 11 (N=4). V. paraibica exhibited a 'steady state' flowering. The species is a day-blooming, and begins to open the flowers around 06:00h.

POLLINATION BIOLOGY: Flowers of Vriesea paraibica show dichogamy with a marked protandry. In the early hours of the anthesis, the stigma is not receptive and is located at the same height as the anthers, but the style gradually extends to reach 4mm above the apex of the anthers.

The yellow, red and green colours of the floral bracts and the yellow corolla seem to be the attractive advertisement for the pollinator.

The septal nectaries have three slits in the gynoecial suture. The petal appendages are lanceolate and touch the base of the style, partitioning the intrafloral chamber into a lower compartment, where the nectar is released.

The volume and sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The volume of nectar in a single flower was 20.2 μl (N = 1) and the mean of concentration of sucrose equivalents was 22% (N = 6, SD ± 0.91, range 16-26%).

The principal visitor of Vriesea paraibica was an unindentified hummingbird, which contacted the stigma during the visits. No other visitors were observed visiting flowers of this species.

BREEDING SYSTEM: Due to the fact that this species occurs in the canopy of tall trees, just two specimens were collected and cultivated in Araras, Petrópolis. The hand-pollinations were performed in previously bagged flowers (N = 4) of two potted individuals and all hand-pollinated pistils from different treatments were fixed at intervals of 48 and 72 hours after pollination. No fruit-set data was obtained.

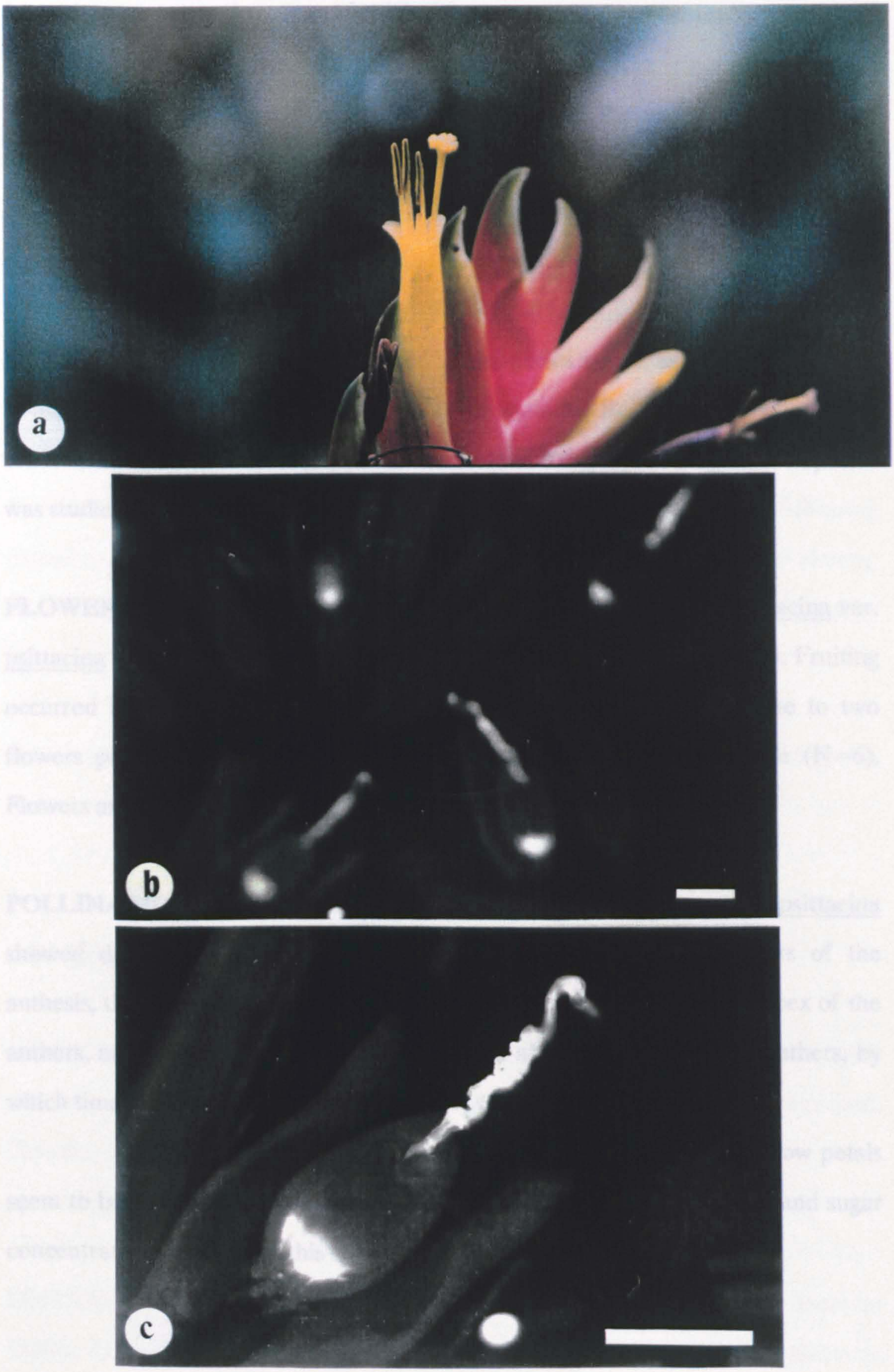
Both self- and cross- hand-pollinated pistils showed that the pollen grain germinated on the stigma and pollen tubes could be distinguished in the style.

The ovules penetration by cross-pollen was higher than the self-pollen at 72 hours interval (SP: mean = 55.2%, N = 2; CP: mean = 86.8%, N = 2). Thus, this species appears to be self-compatible but more pollination experiments are needed to confirm this.

SUMMARY: Vriesea paraibica exhibits 'steady state' flowering phenology, during the months of January and February. It has a diurnal flowering, and is pollinated by hummingbirds in the study area, and appears to be self-compatible.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Nova Friburgo, Ecological Reserve of Macaé de Cima , 30/I/1992, G.Martinelli 14665 (RB).

Plate 5.24. (a) flower of Vriesea paraibica; (b) and (c) penetrated ovules of V. paraibica at 72 hours after self-pollination (scale bars = 100μm).


a
b
c

5.34. Vriesea psittacina (Hooker) Lindley var. psittacina [Tables 5; Figure 5]

MORPHOLOGY: Plant 60cm high when flowering; leaves forming a broadly funnelform rosette. Inflorescence simple with floral bracts red with yellow apices. Flowers with yellow petals, each petal bearing two large, rounded appendages at base, and with the stamens exserted.

DISTRIBUTION AND HABITAT: This species occurs as an epiphytic plant in the lowland and montane wet forests of the Atlantic Rainforest province, from sea level to 900m of altitude, and from Bahia to Rio de Janeiro States. The species was studied in Petrópolis, Rio de Janeiro State.

FLOWERING PHENOLOGY: The flowering period of Vriesea psittacina var. psittacina in the study area, began in December and finished in February. Fruiting occurred between March and April (Figure 5). This species opens one to two flowers per day and presented a mean of 9 flowers per inflorescence (N=6). Flowers are diurnal with the anthesis beginning around 06:00h.

POLLINATION BIOLOGY: Flowers of Vriesea psittacina var. psittacina showed dichogamy with a well-defined protandry. In the early hours of the anthesis, the stigma was not receptive and was located 1mm above the apex of the anthers, and gradually extended to reach 6mm above the apex of the anthers, by which time the stigma became receptive.

The bright red and yellow of the floral bracts and the yellow petals seem to be the important advertisement for the pollinator. The volume and sugar concentration of nectar of this species was not measured.

The visitors of Vriesea psittacina var. psittacina were the hummingbirds Phaetornis petrei and Melanotrochillus fuscus, both visiting with frequency and touching the stigma and the anthers when collecting nectar.

BREEDING SYSTEM: Since just one group of individuals was found growing together, possibly comprising the same genotype, hand-pollination experiments were confined to self-pollination treatments. A sample of selfed pistils were fixed at 24 and 48 hours and were analysed with fluorescence microscopy (N=4).

Pollen tubes from pistils fixed at 48 hous penetrated 23% of ovules (N=4, range 21.4-62.5%). The the natural fruit-set was not obtained.

SUMMARY: Vriesea psittacina var. psittacina exhibits 'steady state' flowering phenology, during the months of December-February. It has a diurnal flowering and was pollinated by the hummingbirds Phaetornis petrei and Melanotrochillus fuscus in the study area. This species seems to be self-compatible.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Petrópolis, Araras, 04/I/1993, G.Martinelli 14718 (RB, cultivated RB, E).

5.35. Vriesea vagans (L.B.Smith) L.B.Smith [Table 5; Figure 5]

MORPHOLOGY: Plant up to 1m when flowering, and propagating by elongate rhizomes. Inflorescence paniculate, few branched and with floral bracts red. Flowers with sepals yellow and petals white, each petal bearing two acute appendages at base, and with stamens and stigma exserted.

DISTRIBUTION AND HABITAT: This species occurs from sea level to 1400m as an epiphyte in moist forest formations of the Atlantic Rainforest province, from Rio de Janeiro State to Rio Grande do Sul. The species was studied in Macaé de Cima Ecological Reserve, Nova Friburgo, Rio de Janeiro State, at 900-1000m of altitude.

FLOWERING PHENOLOGY: The flowering period of Vriesea vagans extended from February to early April. Fruiting occurred in May and June (Figure 5). This species opened up to 4 flowers per day and had diurnal flowers which began to open c. 06:00h.

POLLINATION BIOLOGY: Flowers of Vriesea vagans showed dichogamy with a slight protandry. In the early hours of the anthesis, the stigma was not receptive and was located at the same height as the apex of the anthers, and gradually extended to reach 3mm above the apex of the anthers.

The red floral bracts and the white flowers seem to be the important advertisement for the pollinator. The septal nectaries have three slits in the gynoecial sutures. The petal appendage are acute and touch the base of the style, partitioning off a lower chamber, where the nectar is released.

The sugar concentration of nectar (Table 5) was measured in previously bagged flowers. The mean concentration of sucrose equivalents was 25% (N=4, SD±0.53, range: 24-26%). A unidentified hummingbird was observed visiting the flowers of this species.

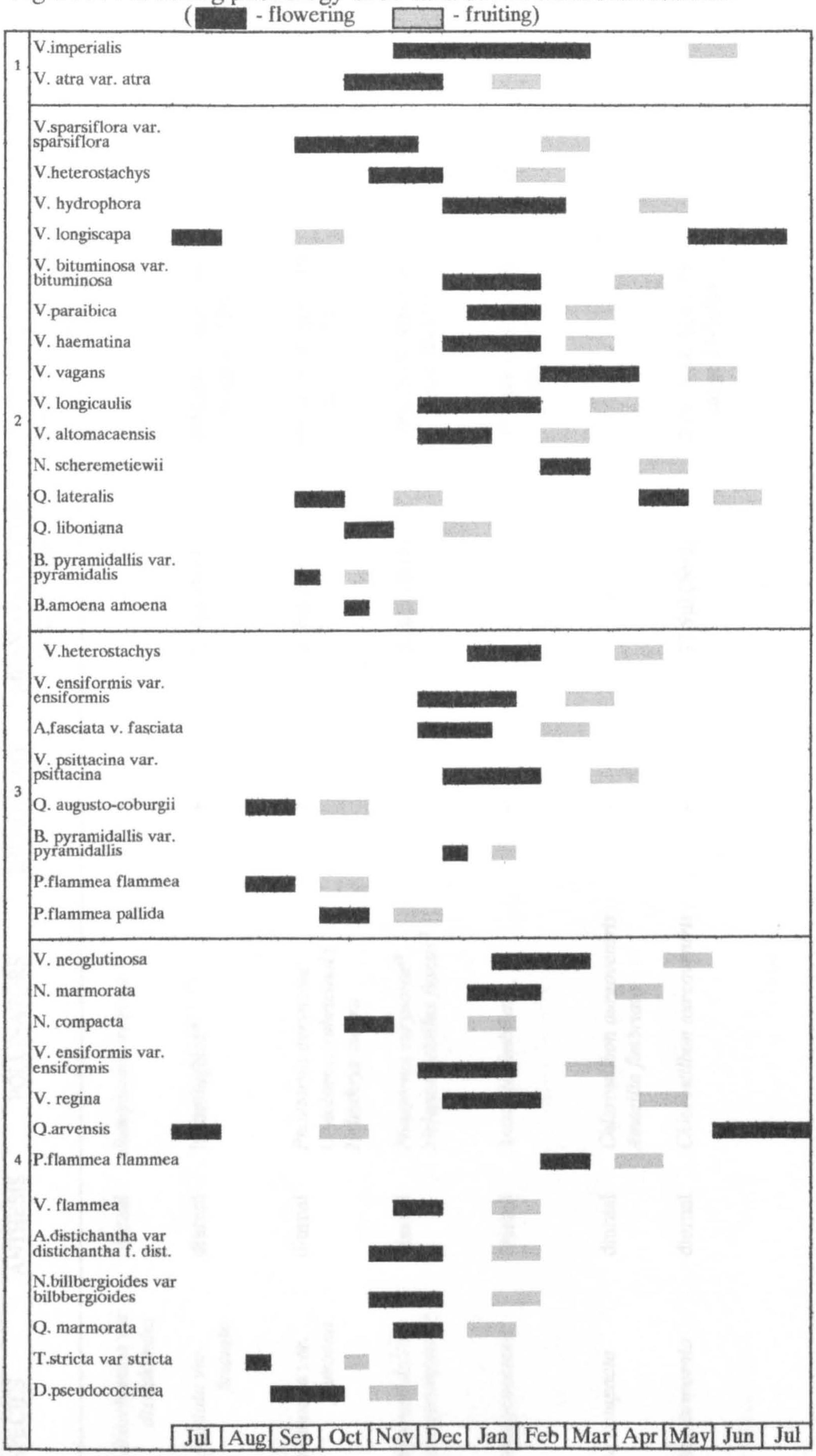
BREEDING SYSTEM: During the period of the field research of this study, it was possible to collect only one flowering individual to cultivate, thus limiting the experiments to the self-pollinations with a small number of flowers. The self-pollinations were performed with previously bagged flowers (N=12) and a subsample of selfed pistils were fixed at 48 hours after pollination. The fruit-set from the other self-pollinated flowers was followed until maturation and showed a relatively low rate of 40% fruit-set (2/5).

Self-pollinated, fixed pistils (N=5) showed that the pollen grains germinated on the stigma and pollen tubes could be distinguished in the style, with 75% of penetrated ovules at 48 hours after pollination (range 69.3-81.2%). This species appears to be self-compatible, but a higher sample of flowers would be necessary to determine this with certainty.

SUMMARY:The flowering period of Vriesea vagans in the area studied was during February-April, presenting diurnal flowers. The species seems to be hummingbird pollinated and appears to be self-compatible.

VOUCHER HERBARIUM SPECIMENS: Rio de Janeiro State: Nova Friburgo, Macaé de Cima Ecological Reserve, 26/IV/1992, G.Martinelli 14693 (RB; cultivated RB, E).

Figure 5. Flowering phenology of 35 taxa of Bromeliaceae studied.



(1) high montane grassland, 1600-1900m; (2) montane wet forest, Macae de Cima, 900-1400m; (3) montane wet forest, Petropolis, 800-1100m and (4) lowland wet forest, restinga and granitic outcrops, Paraty, sea level.

Table 5. Results: pollination biology and breeding systems.

SPECIES	ANTHESIS	POLLINATORS	DICHOGAMY	MEAN VOLUME OF NECTAR (µl)	MEAN SUGAR CONCENTRATION OF NECTAR (%)	BREEDING SYSTEM
Aechmea distichantha var distichantha	diurnal	*Ramphodon naevius*	+	-	-	SI **
Aechmea fasciata var. fasciata	diurnal	hummingbird*	+	15.6µl (N=1)	28% (N=7, SD±2.34, range 22-32%)	SI **
Billbergia amoena var. amoena	diurnal	*Phaetornis eurynome* *Clytolaema rubricauda* *Heliothryx aurira*	+	17.6µl (N=1)	30.6% (N=4, SD±2.19, range 23-32%)	SC **
Billbergia pyramidallis var. pyramidallis	diurnal	*Phaetornis eurynome*[a] *Melanotrochillus fuscus*[b]	+	32.8µl (N=1)	32% (N=8, SD±3.55, range 20-37%)	SI **
Dyckia pseudococcinea	diurnal	*Amazilia fimbriata*	-	-	29% (N=6, SD±4.06, range 24-35%)	SC **
Neoregelia compacta	diurnal	*Chlorostilbon aureoventris* *Amazilia fimbriata*	-	-	-	-
Neoregelia marmorata	diurnal	*Chlorostilbon aureoventris*	-	17.9µl (N=1)	26% (N=4, SD±1.03, range 24-30%)	-

Table 5. Cont.

Nidularium billbergioides var.billbergioides	diurnal	*Chlorostilbon aureoventris*	-	-	-	-
Nidularium scheremetiewii	diurnal	*Heliothryx aurita*	-	-	27% (N=4, SD±3.12, range 19-30%)	-
Pitcairnia flammea var. pallida	nocturnal	hawkmoth (?)	+	60.8µl (N=6, SD±6.03, range 40.8-73.2µl)	12.7% (N=6, SD±3.4, range 8-19%)	SC
Pitcairnia flammea var. flammea	diurnal	*Phaetornis eurynome*[b] *Melanotrochilus fuscus*[b] *Phaetornis aff. petrei*[c] *Amazilia fimbriata*[c]	+	30.7µl (N=1)	17.4% (N=9, SD±4.72, range 11-25%)	SC
Quesnelia arvensis	diurnal	*Chlorostilbon aureoventris* *Amazilia fimbriata*	-	28.6µl (N=2, SD±11.6, range 12.3-28.6µl)	23.8% (N=18, SD±3.63, range 18-29%)	SI
Quesnelia augusto-coburgii	diurnal	*Leucochloris albicollis* *Phaetornis petrei*	-		25% (N=8, SD±1.02, range 21-29%)	-
Quesnelia lateralis	diurnal	hummingbirds (?)	+	11.7µl (N=3, SD±5.16, range 7.7-17.5µl)	30.5% (N=11, SD±3.08, range 24-36%)	SI
Quesnelia liboniana	diurnal	*Phaetornis sp.* *Clytolaema rubricauda*	+	-	-	-

Table 5. Cont.

Quesnelia marmorata	diurnal	hummingbird*	+	27.9µl (N=1)	28% (N=4, SD±1.03, range24-30%)	SI **
Tillandsia stricta var. stricta	diurnal	*Chlorostilbon aureoventris*	-	-	-	-
Vriesea altomacaensis	diurnal	*Stephanoxis lalandi* *Leucochloris albicollis* *Clytolaema rubricauda*	+	-	25.6% (N=4, SD±1.61, range 24-26%)	-
Vriesea atra var. atra	nocturnal	*Anoura caudifer*	+	209µl (N=1)	13.3% (N=6, SD±3.74, range 9-19%)	SC **
Vriesea bituminosa var. bituminosa	nocturnal	bat (?)	+	207µl (N=1)	13.4% (N=6, SD±1.6, range 12-18%)	SC
Vriesea ensiformis var. ensiformis	diurnal	*Melanotrochilus fuscus*[b] *Leucochloris albicollis*[c] *Amazilia fimbriata*[c]	+	32.4µl (N=3, SD±5.98, range 28-42.9µl)	21.9% (N=32, SD±4.68, range 16-30%)	SC
Vriesea flammea	diurnal	*Clytolaema rubricauda*	+	-	-	-
Vriesea haematina	diurnal	*Leucochloris albicollis* *Stephanoxis lalandi* *Clytolaema rubricauda*	+	137µl (N=1)	21.1% (N=8, SD±1.47, range 19-23%)	SC **

Table 5. Cont.

Vriesea heterostachys	diurnal	*Leucochloris albicollis*	+	-	27.4% (N=14, SD±3.32, range 20-31%)	SC
Vriesea hydrophora	nocturnal	bat/hawkmoth (?)	+	90.8µl (N=1)	13% (N=13, SD±2.25, range 7-15%)	SC
Vriesea imperialis	nocturnal	*Anoura caudifer*[ab] *Artibeus lituratus*[ab]	+	168.26µl (N=4, SD±49.9, range 121-228µl)	15.6% (N=28, SD±3.62, range 12-23%)	SC
Vriesea incurvata	diurnal	*Amazilia fimbriata*	+	32.58µl (N=1)	22.2% (N=5, SD±1.73, range 19-30%)	SC
Vriesea longicaulis	nocturnal	bat/hawkmoth (?)	+	-	17% (N=4, SD±2.12, range 16-20%)	SC **
Vriesea longiscapa	nocturnal	bat/hawkmoth (?)	+	-	15.9% (N=23, SD±2.04, range 8-19%)	SC
Vriesea neoglutinosa	diurnal	*Amazilia fimbriata* *Chlorostilbon aureoventris*	+	63.3µl (N=6, SD±16.8, range 54.9-85.3µl)	19.8% (N=27, SD±2.9, range16-28%)	SC
Vriesea paraibica	diurnal	hummingbird*	+	20.2µl (N=1)	22% (N=6, SD±0.91, range 16-26%)	SC **
Vriesea psittacina var. psittacina	diurnal	*Phaetornis petrei* *Melanotrochilus fuscus*	+	-	-	SC **

Table 5. Cont.

Vriesea regina	nocturnal	*Anoura caudifer* *Anoura geoffroy* *Artibeus lituratus* *Glossophaga soricina*	+	218µl (N=1)	12.4% (N=21, SD±3.86, range-8-20%)	SC
Vriesea sparsiflora var. sparsiflora	diurnal	*Stephanoxis lalandi* *Clytolaema rubricauda* *Leucochloris albicollis* *Phaetornis eurynome*	+	19.6µl (N=11, SD±7.4, range 12.9-22.7µl)	22.7% (N=23, SD±3.09, range 17-27%)	SC
Vriesea vagans	diurnal	hummingbirds*	+	-	25.1% (N=4, SD±0.53, range 24-26%)	SC **

* unindentified species
** results based on few samples, needs to be confirmed
[a] observed in the population of Macaé de Cima Ecological Reserve
[b] observed in the population of Araras, Petrópolis
[c] observed in the population of Paraty
(?) need to be confirmed

CHAPTER 6. DISCUSSION

6.1. FLOWERING PHENOLOGY

Flowering plant phenology has been studied from the point of view of pattern (Gentry, 1974; Bawa, 1983), seasonality and climatic control (Janzen, 1967; Frankie et al., 1974; Augspurger, 1980) and interspecific competition between individuals of different species sharing the same pollinators (Levin & Anderson, 1970; Stiles, 1975, 1977, 1978; Pool & Rathcke, 1978; Waser 1978; 1983).

Gentry (1974) in a study of flowering in Central American Bignoniaceae provided a classification of flowering 'strategies' in that family in which he recognized four types of flowering phenology: (1) 'steady state', with plants producing relatively few flowers per day over extended periods of several months or more; (2) 'cornucopia' with the plants producing large number of flowers daily over a time span of several weeks; (3) 'big-bang' in which the plants in an area have a very precise synchronization so that so they come into flower for a relatively brief time of a few days; and (4) 'multiple bang' in which plants in the population come into flower repeatly, more or less in synchrony, for periods of few days. This type of classification has a general applicability to other families, although Gentry's original paper presents some difficulties of interpretation since the 'x' axis on his flowering pattern diagrams (Gentry, 1974, Fig. 2) gives "number of flowers" (without any explanation of how established) whereas the criteria for the various types can differ in emphasis. Thus, for the 'steady state' and also to some extent the 'cornucopia' type, the flowering pattern of individual plants in the population is important (number of flowers over period of time), for both 'big bang' and 'multiple bang' strategies, the number of individuals which come into synchronized flowering over short periods is the important criterion, although most species of this type are also mass flower producers.

In the present study of 35 species of Bromeliaceae the great majority of species clearly fall into the 'steady state' type phenological pattern or strategy, since individual plants in populations of 22 species (62.8%) produce c. 2-4 or so flowers per day (or night) over periods of 20 days or so (e.g. Vriesea bituminosa var. bituminosa, V. ensiformis var. ensiformis, V. incurvata, among others). Another 13 species (37.2%) show a 'cornucopia' type of flowering, they open 3-8 flowers per day, as flowering proceeds, so that each plant may open many flowers per day over a period of 3-10 days (e.g. Quesnelia augusto-coburgii, Quesnelia marmorata, Pitcairnia flammea var. flammea).

Two species, Billbergia pyramidallis var. pyramidallis and B. amoena var. amoena, were also considered to have a 'cornucopia' type phenology, since individual plants open flowers through the entire inflorescence over a period of 2-4 days. However, in both species there is a relatively low synchrony between individuals of the population, such that flowering of all plants may extended over 8-12 days.

In the seasonal tropical forests of South America, flowering may be 'peaked' to the end of the dry season-early rainy season period (Janzen, 1967). It should be noted, however, that peaked flowering is not so evident in for example the seasonal vegetation of 'cerrados' of Central Brazil, since many species flower at other times of the year (Oliveira, 1991). Some studies have correlated the onset of flowering at the end of the dry season with climatic cues, e.g. increases in relative humidity for some myrtaceous species (Proença & Gibbs, 1993), or arrival of the first rains (Augspurger, 1980). In the so-called 'non-seasonal' humid forest it is now recognized that there may also be, albeit more subtle, climatic cues for flowering (Stiles, 1978; Bawa, 1983). In the montane Atlantic Rainforest of SE Brazil there occurs a distinct fluctuation with rainfall pattern and temperature, between a

November-March 'summer' season, with rainfall over 200mm per month, and temperature averaging c. 27° C, and a 'winter' season, with rainfall up to 60mm per month and temperature averaging c. 12° C. It is notable that the flowering phenology of bromeliad species in these areas shows a distinct displacement towards the wet, summer period, with the majority of species in flower between November-February (Figure 5; Table 6.1). In fact, 73% of the species studied in the areas at Macaé de Cima and Petrópolis flowered in this period. In contrast, only seven species (23%) were in flower at these localities during the months of April-September.

One probable explanation for the lack of flowering species during the 'winter' months is the cool night temperatures which prevail at this time. Although hummingbirds are warm blooded vectors, and therefore able to function at cooler temperatures, they encounter problems with the regulation of torpor. This is a physiological state of lowered metabolism which permits hummingbirds to pass cold nights at low energy consumption. However, emerging from torpor the following morning has a high energy consumption cost and ideally needs a warm day temperature (Heinrich, 1983; Sick, 1988). It is possible that the cool, misty days prevailing in the Serra do Mar during the 'winter months' are limiting for many hummingbirds species. Certainly, during fieldwork at Macaé de Cima I have observed a diminished number of birds, including hummingbirds, and also primates, in this area during the months of May-August, and these animals are likely to migrate to lower altitudes during this period.

Another feature of the seasonal climate in the Serra do Mar is that whilst the summer rains often fall as brief but torrential storms, those of the winter are more prolonged and of a fine, often drizzle-like nature. Also the cloud base is often low giving mist conditions at this time. These conditions are reflected in the relative humidity values (Table 3.2.1, 3.2.2), such that despite the lower volume of rain during March-August, the relative humidity is actually higher during these months. Again, such cool mists and continuous drizzly rain are probably inimical to pollinator activity.

At Paraty, the climate is much more equable and mean temperatures scarcely fall bellow 20° C (Table 3.2.3). The fact that flowering at this site was also skewed towards the summer months of November-March is probably an artefact, due to the fact that overall fewer species were studied in this area (see Material and Methods), over more irregular intervals, and most species were from exposed granitic outcrops or restinga vegetation near the sea.

Table 6.1. Total number of species in flowering by months in the three areas of study.

MONTHS	% OF SPECIES IN FLOWER: ALL SITES (35)	MACAÉ DE CIMA (16)	PETRÓPOLIS (10)	PARATY (13)
JAN	42.8%	7	5	4
FEB	40%	8	3	4
MAR	14.3%	3	1	2
APR	5.7%	2	-	-
MAY	5.7%	2	-	-
JUN	5.7%	1	-	1
JUL	5.7%	1	-	1
AUG	8.6%	-	2	1
SEP	17.1%	3	2	1
OCT	22.8%	4	2	2
NOV	28.6%	4	2	5
DEC	51.4%	7	6	6

Notes:

1. Vriesea imperialis, V. heterostachys, Billbergia pyramidallis var. pyramidallis and Pitcairnia flammea var. pallida were counted in both areas which they were studied.
2. Quesnelia lateralis was counted twice, since that it flowered in two periods (April-May and September-October), in different localities.
3. The high number of species flowering in Macaé de Cima reflects the high number of taxa included in this area, 45.7% of the total number of species studied.

A phenomenon which has been debated in flowering phenology studies is whether flowering displacement occurs between species of a community which share the same pollinator or pollinator guild. The basic concepts of this situation are relatively simple: where two or more species share the same pollinator, either or both species might be expected to suffer a diminuition of reproductive success due to (1) so-called 'exploitation competition', where one species suffers insufficient pollinator visits, with little pollen transferred to stigmas, due to the superior attraction/reward of flowers of the other species; or (2) by 'interference competition', where pollinators visiting flowers of several different species bring mixed pollen loads to the stigmas (Waser, 1983). In these circumstances, an adaptative strategy to restore maximum reproductive success might be for the species of the community to show displaced or sequential flowering, such that the pollinator(s) is shared with minimum competitive effects. Robertson (1895) published a pioneer paper on this theme, with reference to the early spring herbaceous flora of an Illinois woodland community. Mosquin (1971) also produced a seminal paper for species of the Alaskan flora, and there have been many other contributions (e.g. Carpenter, 1976; Stiles, 1975; Waser, 1978).

However, it has proved difficult to establish an adaptative element in most studies of alleged competition induced displaced flowering studies, and more recently most authors have been critical of this phenomenon (see Waser, 1983 for review). Poole & Rathcke (1979), compared Stile's (1977) data from a community of ten tropical hummingbird pollinated plants with a statistically generated null hypothesis. They asked whether peak flowering times for these species were regularly spaced through the normal season, and concluded instead that flowering peaks were significantly clumped during two yearly dry periods. From this they argued that there was no clear reason to implicate competition for pollination as a force that had produced flowering time differences. Similarly, Kochmer & Handel (1986), made a large-scale comparison of flowering times in the flora of North and South Carolinas, U.S.A., with that of a similar area in temperate Japan, with a similar climate. These authors found a marked phylogenetic correlation in the flowering periods of different taxa in the two areas, and were therefore sceptical of the role of pollination competition as an influence on flowering phenology.

Although most studies on pollinator sharing have emphasized the deleterious effects of pollination competition, some studies have proposed that synchronous flowering in species sharing the same pollinator may be beneficial. Thus, Schemske (1981) presented evidence to support the view that two species of Costus in Central America, C. allenii and C. laevis, which share the same euglossine bee pollinator (Euglossa imperialis), benefit in terms of enhanced fruit-set from flowering synchronously.

In the present study, despite the fact that most species are pollinated by hummingbirds, many bromeliad species have overlapping flowering periods with little evidence of adaptative phenological displacement. And, the relatively high levels of fruit-set shown by most of these species gives little indication of lowered fruit-set due to pollinator competition. In this context it is important to note that although many of these species are self-compatible, floral mechanisms such as marked protandry mean that flowers must be visited by a vector even to effect self-pollination. Good fruit-set, therefore indicates effective levels of pollination visitation in these bromeliads.

6.2. POLLINATION BIOLOGY

Given the emphasis in the literature on hummingbirds as pollinators of Bromeliaceae species (Table 2.1) it is not surprising that the principal pollinators of bromeliad taxa in the Atlantic Rainforest observed in these present study were hummingbirds (Table 5). Of the 35 species monitored for pollinators, 26 were established as hummingbird pollinated, and one more species is likely, on grounds of diurnal anthesis, floral morphology and nectar characteristics, to have this type of vector, giving a total of 77.1% of the studied species.

Of the 26 confirmed hummingbird-pollinated species, 11 belong to the genus Vriesea, and the others to diverse genera: Aechmea (2), Billbergia (2), *Dyckia* (1), *Neoregelia* (2), *Nidularium* (2), *Pitcairnia* (1), *Quesnelia* (4) and *Tillandsia* (1). These genera include both epiphytes and terrestrial taxa, and occur in all study sites and vegetation types.

A total of 15 species of hummingbirds were observed visiting these 26 bromeliad in the study areas. Of those vectors, seven hummingbirds were only observed at Paraty, three were observed only in Petrópolis, and likewise three only at Macaé de Cima. Only one hummingbird (*Leucochloris albicollis*) was seen at all three sites, whilst the hermit hummingbird species *Phaetornis eurynome* was seen as a pollinator at the two upland sites, Petrópolis and Macaé de Cima. Some 14 species of bromeliad were observed to be visited by only a single species of hummingbird (*Aechmea distichantha* var. *distichantha*, *Aechmea fasciata* var. *fasciata*, *Dyckia pseudococcinea*, *Neoregelia marmorata*, *Nidularium billbergioides* var. *billbergioides*, *Nidularium scheremetiewii*, *Quesnelia marmorata*, *Tillandsia stricta* var. *stricta*, *Vriesea flammea*, *V. heterostachys*, *V. incurvata*, *V. paraibica* and *V. vagans*), whilst at the other extreme, four bromeliads were visited by three or more species of hummingbirds: *Billbergia amoena* var. *amoena* (3), *Vriesea altomacaensis* (3), *V. haematina* (3) and *V. sparsiflora* var. *sparsiflora* (4).

In terms of pollinator sharing, between synchronously flowering species, this was observed for some taxa at all study sites. Thus, at Macaé de Cima, *Vriesea sparsiflora* var. *sparsiflora* and *V. heterostachys*, both flowering in November, shared *Leucochloris albicollis*, but whilst this was the only visitor to *V. heterostachys*, *V. sparsiflora* var. *sparsiflora* was also visited by *Stephanoxis lalandi* and *Clytolaema rubricauda*. Similarly, at Araras (Petrópolis) *Vriesea ensiformis* var. *ensiformis* and *V. psittacina* var. *psittacina*, both in flower in January, were both frequented by *Melanotrochillus fuscus*, but *V. psittacina* var. *psittacina* was also visited by *Phaetornis eurynome*. At Paraty, *Vriesea neoglutinosa* and *V. ensiformis* var. *ensiformis* were both visited by *Amazilia fimbriata*, although the former bromeliad was also visited by *Chlorostilbon aureoventris* whilst *V. ensiformis* var. *ensiformis* was also visited by *Leucochloris albicollis*.

Two rare examples of intergeneric sharing of pollinator occurred at this site, where Chlorostilbon aureoventris visited Vriesea ensiformis var. ensiformis and Neoregelia marmorata, and likewise, Amazilia fimbriata visited Vriesea neoglutinosa and Pitcairnia flammea var. flammea in February-March. In general, however, synchronously flowering species of different genera were visited by different hummingbirds. However, in different months, the same hummingbird species might visit several different bromeliad genera e.g. at Paraty, Amazilia fimbriata frequented Quesnelia arvensis in July, Vriesea ensiformis var. ensiformis in December-January, and Pitcairnia flammea var. flammea in February-March.

Non-hermit hummingbirds (Trochilinae) were the most common group in all studies sites, with the species Amazilia fimbriata, Clytolaema rubricauda and Chlorostilbon aureoventris the most frequent, visiting a wide array of different species during their foraging, including species for which the length of the corolla was longer than their beaks. These hummingbirds seem to be well adapted generalists to flowers of Bromeliaceae. In contrast, Stephanoxis lalandi was observed to be restricted to the montane wet forest at altitudes up to 1000m and appeared to be a effective or potential pollinator for the flowers of several species in this area.

Hermit hummingbirds were represented by the species Phaetornis euronyme, Phaetornis petrei, and Phaetornis sp., which appeared to be somewhat more selective in their flowers, when compared with non-hermit hummingbirds, since they mostly visited bromeliad species with long-tubular and slightly curved flowers such as those of Vriesea sparsiflora var. sparsiflora, Billbergia amoena var. amoena, B. pyramidallis var. pyramidallis, Quesnelia augusto-coburgii, Quesnelia liboniana and Pitcairnia flammea var. flammea. All of these species have concealed nectaries so that the nectar may only be accessible to such hermit hummingbirds which have long and slightly curved beaks.

Hummingbird flowers have been associated with red flowers by several authors (e.g. Ruschi, 1982; Sick, 1984; Prance 1985), but other authors have criticised this view (e.g. Bene, 1941; Grant, 1966) arguing that hummingbirds have no innate preferences for red but rather the prominence of red flowers among hummingbird visited flowers is a learned preference. Of the 26 hummingbird pollinated species in the present study, 18 has red bracts usually contrasting with blue, yellow or white of the corolla, and six have rose or orange bracts. Only one hummingbird-pollinated species, Vriesea altomacaensis has yellow corolla with no red colouration of bracts. Thus, whether the preference for red is innate or learned, bromeliads certainly support the view that hummingbird flowers are commonly red in colour.

Sugar concentration of the nectar (Baker, 1975; Pyke & Waser 1981), the composition of sugars in the nectar (Baker & Baker, 1983; Stiles & Freeman, 1993), and the rate of nectar production (Pleasants, 1983), are the most important propieties of nectar as a reward offered to potential pollinators in angiosperms. Baker (1975) presented data of sugar concentration of nectar of 30 hummingbird-pollinated species of Costa Rica of three ecologically different areas in two altitudinal zones: dry forest and savanna of Guanacaste, at 100m, in which the mean concentration of sucrose equivalents was 24% (N=8, range 12-31%), montane wet forest at 1000-2000m with a mean of 21% (N=10, range 16-29%), and Finca La Selva, at 140m, which he found 20% of mean of sugar concentration for the hummingbird-flowers (N=12, range 14-29%).

Stiles & Freeman (1993) studied the patterns of floral nectar in 120 hummingbird-visited species in Costa Rica, including the bromeliad Aechmea mariae-reginae. In this latter species they found a mean sugar concentration of 23% (0.75 M) with a daily nectar secretion of 20μl.

In these studies, the average sugar concentration of nectar of hummingbird-pollinated species was somewhat low at c. 21%. Although some authors (e.g. Percival, 1965), predicted that large-bodied vectors such as birds or bats require concentrated sugar values, Baker (1975) has argued that empirical studies have shown that this is not the case, and that because of the particular correlation between sucrose concentration and viscosity there are good theoretical reasons why this should not be so. Seemingly, the viscosity of sucrose solution rises virtually exponentially with concentration, so that nectar with concentration over 35% would become increasingly difficult for hummingbird ro retrieve rapidly from the flower.

Thus, although Bernardello et al. (1991), who studied the nectar of 29 species of Argentinian bromeliads, including six apparently hummingbird pollinated species, for which nectar concentration of 25-48% (mean 36%) were found, the present study of Atlantic Rainforest bromeliads tends to confirm the view that the nectar of hummingbird flowers is relatively dilute.

The mean concentration of sugar for hummingbird-pollinated species which occur in the montane wet forest, between 800-1500m was 25.4%, (N=14, range 17.4-32.2%), compared with species which occurs at sea level (23.5%, N=8, range17.4-29) was not significant. The species Pitcairnia flammea var. flammea, which have population in both areas was included in the counting of both cases and showed no significant difference of sugar concentration between the population at the two different altitudinal zones (Paraty: 17.4%, N=9, range 11-25% and Petrópolis: 18.4%, N=32, range 16-30%, respectively).

Chiropterophily in Bromeliaceae had been confirmed in two species of the subfamily Tillandsioideae: Vriesea morrenii (Vogel, 1969) and V. irazuensis (Salas, 1973) and in only one species of the subfamily Pitcairnioideae: Encholirium glaziovii (Sazima et al., 1989), but had been speculatively suggested for some other species on the basis of their floral morphology, by several authors as Vogel (1969), Utley (1983), Rauh (1986) and Varadarajan & Brown (1988), to give a total of 31 species suggested as bat-pollinated, 27 of these in the genus Vriesea (Tillandsioideae), and the remaining for species of the genera Ayensua (1), Encholirium (1), Pitcairnia (2) and Puya (2), all of the subfamily Pitcairnioideae. No species belonging to the subfamily Bromelioideae have been reported or suggested to be bat-pollinated (see Table 2.1).

In the present study, seven species belonging the genus Vriesea were considered to be pollinated by bats (Table 5), three of them confirmed with bats as visitors of the flowers: V. atra var. atra, V. imperialis and V. regina, and with bat-pollination suggested for the four species: V. bituminosa var. bituminosa, V. hydrophora, V. longicaulis and V. longiscapa, on the grounds of floral morphology, nocturnal anthesis and presence of floral scent or odour. However, no bats were observed visiting these species despite several hours of nocturnal observation.

The common characteristics of all of these species were the nocturnal anthesis, the presence of odour in the flowers, the high volume of nectar (mean = 178.6μl, N = 5, range 90.8-218μl) and the relatively low sugar concentration of nectar (mean = 14.4%, N = 7, range 12.4-17%).

These bat-pollinated species can be divided in two distinct groups according to their habit, floral morphology, flowering phenology and the distribution and size of populations: (1) the two saxicolous species Vriesea imperialis and V. regina with flowers which have spirally recurved petals during the anthesis thus exposing the stamens and style (brush-like type). These species have episodic flowering in intervals of 2-3 years, and populations formed by a large number of densely grouped individuals; and (2) epiphytic species with tubular flowers with the filaments and style included in the corolla, and an annual flowering of 'steady state' type, and occurring in small populations of scattered dispersed individuals (Vriesea atra var. atra, V. bituminosa var. bituminosa, V. hydrophora, V. longicaulis and V. longiscapa).

Only one species of bat (Anoura caudifer) was observed to visit flowers of Vriesea atra var. atra, whereas in V. imperialis two species of bat were observed (Anoura caudifer and Artibeus lituratus), and in V. regina four species visited the flowers (Anoura caudifer, Anoura geoffroy, Artibeus lituratus and Glossophaga soricina).

6.3 BREEDING SYSTEM

Breeding systems in flowering plants can be viewed as the combination of factors which control the level of genetic recombination which takes place within species populations. Thus, on a broad interpretation, components of the breeding system include: the pollination system (e.g. type of vector and its ability to disseminate pollen in the population), seed dispersal mechanisms, and cytological aspects such as chromosome number and chiasma frequency. But the principal component is the extent to which inbreeding or outbreeding takes place, mainly modulated by whether plants are capable of self-pollination and self-fertilization (i.e. autogamous) or are cross-pollinated and cross-fertilized (i.e. allogamous). Between these two extremes, a whole range of 'mixed-mating' situations may occur. The level of outbreeding vs. inbreeding can be controlled the presence of self-incompatibility mechanism in plants with hermaphrodite flowers, or by various unisexual flower strategies, such as monoecy, gynodioecy and dioecy, among others.

Traditionally, because on a neo-Darwinian view of evolution it has been accepted that levels of genetic heterogeneity in populations permit evolutionary flexibility and therefore evolutionary success, selective pressures to optimise the level of recombination have been regarded as the only force controlling the components of the breeding system (Darlington, 1958; Grant, 1958). More recent authors have moved away from this concept somewhat, and the term 'sexual system' has been substituted for breeding system, and various models have been proposed which do not involve optimisation of outcrossing as a primary selective agent (Maynard Smith, 1978; Charnov, 1979; Willson, 1979; Bawa, 1974; see Bawa & Beach, 1981 for review). Table 6.3.1. provides a fairly standard classification of sexual systems in flowering plants, modified from Bawa & Beach (1981).

Table 6.3. Classification of flowering plant sexual systems*.

A. Systems based on the spatial distribution of male and female reproductive organs.	
Sexually monomorphic: one gender class of individuals	Sexually dimorphic: two gender classes of individuals
hermaphroditism: only bisexual flowers Monoecism: male and female flowers Andromonoecism:bisexual and male flowers Gynomonoecism: bisexual and female flowers	Dioecism: male or female flowers Gynodioecism: female or bisexual flowers Androdioecism: male or bisexual flowers
B. Systems based on temporal distribution of male and female organs	
Protandry: anthers release pollen before the stigma becomes receptive	Protogyny: stigma becomes receptive before anthers release pollen
C. Systems based on the presence or absence of self-incompatibility alleles	
Self-incompatibility (SI): presence of self-incompatibility alleles between pollen and stigma; self-pollination results in no fruit-set. Homomorphic and heteromorphic systems (including distyly and tristyly)	Self-compatibility (SC): without presence of self-incompatibility alleles; cross- and self-pollination result in fruit-set.

* Modified from Bawa & Beach (1981).

Evidently, the systems are not mutually exclusive, such that, for example, many Bromeliaceae species combine hermaphroditism with protandry with self-compatibility. Given that the majority of angiosperm species have hermaphrodite flowers (associated with efficiency of pollen transfer by animal vectors but also permitting the possibility of self-pollination) the presence or absence of genetic self-incompatibility mechanisms is an important factor controlling outcrossing.

Three main self-incompatibility systems have been established in the flowering plants: homomorphic, gametophytic self-incompatibility (GSI), homomorphic, sporophytic self-incompatibility (SSI), and heteromorphic self-incompatibility (HetSI) (Nettancourt, 1977; Gibbs, 1986; Barrett, 1988).

Homomorphic systems have a single multiallelic locus (*S*) with multiple alleles controlling incompatibility, and heteromorphic systems, in which distyly is controlled by a single locus with two alleles, and tristyly which present two loci each with two alleles, with epistasis operating between the loci (Gibbs, 1986; Barrett, 1988).

A more recent development has been the appreciation that other, more enigmatic mecanisms may occur, in which selfed flowers may be uniformly rejected despite the fact that self-pollen tubes reach the ovary and may penetrate ovules. Such phenomena have been variously referred to as late-acting self-incompatibility (LSI) (Seavey & Bawa, 1986; Gibbs & Bianchi, 1993) or cryptic self-fertility (Bertin & Sullivan, 1988).

For homomorphic, sporophytic self-incompatibility (SSI), the genetic model proposed suggests a single locus *S* with multiple alleles in the population, and the allelic constitution of the pollen-producing plant determines the incompatibility reaction of the pollen. Of the classic self-incompatibility systems, SSI is the most restricted in occurrence, having been well studied in only two families, the Compositae and Cruciferae, but also probably present in the Convolvulaceae (Ipomoea sp.) and Betulaceae (Coryllus avellana) (Gibbs, 1986, 1988). This mechanism is associated with the presence of three-celled pollen, a site of incompatibility reaction at the stigmatic surface (i.e. self-pollen grains either do not germinate on the stigma, or their pollen tubes do not penetrate the stigmatic papillae, and papilla cells adjacent to incompatible pollen grains frequently show callose deposition at their tips). Homomorphic sporophytic SI has not been reported in any monocotyledonous families to date.

Heteromorphic self-incompatibility (HetSI), also involves a "sporophytic" mechanism with the reaction of the pollen determined by the genotype of the parent sporophyte. This system is associated with distyly and tristyly which occurs in 24 families of Angiosperms (Ganders, 1979). The site of incompatibility reaction is variable and may be located in the stigmatic papillae or the upper style or even the ovary. Heteromorphic SI is of fairly widespread but of scattered occurrence (Ganders, 1979), and is known in monocot families such as the Iridaceae and Pontederiaceae. The presence of this mechanism is usually evident on account of the associated floral morphs (commonly long- vs. short style) and no evidence of its occurrence in the Bromeliaceae is known.

Homomorphic gametophytic SI is the most widespread of these mechanisms, and is known to occur in a number of monocotyledonous families such as the Liliaceae, Commelinaceae, Gramineae, among others (Nettancourt, 1977). The site of the rejection proccess in GSI is rather variable (Gibbs, 1986) but commonly manifest between pollen tubes and the cells of the stylar transmitting tract such that incompatible pollen tubes are arrested in growth in the upper to mid-stylar region. If SI occurs in the family Bromeliaceae, a priori it is most likely to be of the GSI type, although LSI cannot be ruled out.

Very little has been published on the breeding systems of the Bromeliaceae, despite this being large neotropical family with considerable horticultural interest (Kress, 1986; Gentry & Dodson, 1987). The literature reports of comments on breeding systems of Bromeliaceae have been summarized by McWilliams (1974) and most of them were based on observations of floral structure and fruit-set in isolated plants in cultivation rather than being derived from controlled pollination experiments. Only the study of Brewbaker & Gorrez (1967) with Ananas comosus attempted to elucidate the nature ofthe SI.

The list of putative breeding systems of Bromeliaceae suggested by previous authors (Table 2.2) indicates that self-compatibility is probably widespread in all three subfamilies. Exceptions seem to be in the subfamily Tillandsioideae, with Tillandsia ionantha (Soltis et al., 1987) although no direct observations of compatibility were undertaken via controlled pollination experiments for this species, but rather the breeding system was predicted on the basis of genetic structure deduced from allozyme frequencies; and the subfamily

Bromelioideae with *Ananas comosus* (Brewbaker & Gorrez, 1987). In the subfamily Pitcairnioideae no SI species have been reported.

Some bromeliad species ensure outbreeding by means of dioecy. This breeding system is found in some species of *Catopsis* (Tillandsioideae), although this genus also has some hermaphroditic species, and the xerophytic genus *Hechtia* (Pitcairnioideae) is reported to have 49 dioecious species (Brown & Gilmartin, 1989). The presence of dioecy in Tillandsioideae and Pitcairnioideae can be considered as derived system, since dioecy has been observed to arise in species with diminutive flowers, as in *Catopsis* and *Hechtia*, which are probably pollinated by small and promiscuous insects, and by the fact that pollination by such pollinators results in high level of selfing in self-compatible species, as hypothesized by Lloyd (1982).

In the 35 species reported in this study, 26 were investigated by means of controlled self- vs. cross-pollinations, and 14 of these were further investigated with a combination of fluorescence microscopy studies of post-pollination events in the stigma and the style, coupled with assessment of fruit-set in hand-pollinated flowers. A further 12 species were studied in less detail, usually due to constraints of time, or insufficient plants to constitute a 'mini-population' in cultivation. For most of these latter species, self-pollinations, usually with some fixations of pistils for studies of pollen tube growth at 48, 72 and 96h, were the only studies undertaken.

For the over-whelming majority (20) of these 35 species, self-compatibility is indicated by the presence of massive self-pollen tube growth in the style and many penetrated ovules in the ovary, and also for those species studied in more detail, from fruit-set in self-pollinated flowers. These 20 species comprise 16 taxa of the subfamily Tillandsioideae, three of the subfamily Pitcairnioideae, and one of Bromelioideae.

However, for 7 species, comprising *Aechmea distichantha* var. *distichantha*, *Aechmea fasciata* var. *fasciata*, *Billbergia pyramidallis* var.

pyramidallis, Quesnelia arvensis, Quesnelia lateralis and Quesnelia marmorata, self-incompatibility is indicated, although some of these taxa fall into the category of species for which limited experimental pollination studies were carried out so that their SI status requires more detailed work for absolute confirmation. In all of these species, although self-pollen germinated on the stigma, self-pollen tubes barely entered the upper style, and certainly no growth to the ovary was observed.

It is of interest that all of these species are members of the subfamily Bromelioideae, and the only other bromeliad species known to be SI on the basis of detailed experimental studies is Ananas comosus (Brewbaker & Gorrez, 1967), also of this subfamily. Moreover, from observations of isolated plants failing to set fruit in cultivation, McWilliams (1974) concluded that Aechmea fulgens and Aechmea nudicaulis were outbreeders.

Also of interest is the fact that in most of these genera which have some SI species (Aechmea, Billbergia and Quesnelia), some self-compatible species are also reported. Thus, in the present study, Billbergia amoena var. amoena was probably self-compatible (a second rank species), and McWilliams (1974) reported all species of Billbergia subgenus Helicoidea to be 'inbreeding' as opposed to species of subgenus Billbergia which were listed as 'outcrossing'. (However, in the present study, the SC taxon Billbergia amoena var. amoena and the SI taxa Billbergia pyramidallis var. pyramidallis both belong to the subgenus Billbergia). Likewise, Brewbaker & Gorrez (1967) established that whilst Ananas comosus is a self-incompatible species, two other species of this genus, Ananas ananassoides and Ananas bracteatus, were found to be self-compatible.

The occurrence of congeneric self-compatible and self-incompatible species can often be correlated with life-form or habitat characteristics. Short-lived ephemerals are often selfing taxa, whereas long-lived perennials are wholly self-incompatible outbreeders (Stebbins, 1950). However, with regard to the self-compatible vs. self-incompatible species of the genera Aechmea, Billbergia, Quesnelia and Ananas, no obvious differences in habitat, pollination and longevity are evident. All of these species are terrestrial or epiphytic, monocarpic, bromeliad species which are pollinated by hummingbirds. But this contrasts with the study by Soltis et al. (1987) who looked at genetic variation in two species of *Tillandsia*, *T. ionantha* and *T. recurvata* which do differ in habitat: *T. ionantha* is found in semi-xeric habitats, whereas *T. recurvata* occurs is drought stressed areas. Moreover, these species differ in flower structure, with *T. ionantha* having largish corollas with exserted anthers and stigmas, whilst *T. recurvata* has reduced flowers with included anthers and stigmas. Allozyme studies on several populations of each of these species indicated that they differ in their breeding systems, with *T. ionantha* seemingly an outcrossing species, or at least one with mixed mating, whilst *T. recurvata* showed high levels of inbreeding. No hand-pollinations experiments were performed with either species, so that it is not known whether *T. ionantha* is genetically self-incompatible. If this should prove to be the case, it would be the first species of the subfamily Tillandsioideae to be established as SI, and the first species of bromeliad outside the subfamily Bromelioideae with SI.

Murawski & Hamrick (1990) have also investigated the genetic and clonal structure of a terrestrial bromeliad, *Aechmea magdalenae*, growing on Barro Colorado Island, using electrophoretic analyses of isozyme variation. Again, no experimental pollinations were carried out to establish whether genetic self-incompatibility is present in *Aechmea magdalenae*, and the results from the isozyme study of nine populations are rather equivocal on this point. Thus, for the nine populations as a whole, 33% of the loci were polymorphic, and the genetic diversity was 0.21, whereas within populations, the mean genetic diversity was 0.084. As these authors comment, at this latter, populational level, *A. magdalenae* is less variable than e.g. the average proportion of polymorphic loci for monocots at 40.3%, or long lived herbaceous perenials at 39.3%, or tropical trees 32.7%. But *A. magdalenae* is more variable within populations than both *Tillandsia* species, *T. ionantha* and *T. recurvata* reported by Soltis et al. (1987). It is possible that *A. magdalenae* has a mixed mating system, but the patchy nature and relative small populations of this species, in which a founder principal will be important, will also effect the genetic structure of this species.

On this point, it is important to stress that the presence or absence of a self-incompatibility mechanism is not an absolute indicator of high vs. low genetic heterozygosity. Thus, an SI species which occurs in small populations, likely to be derived from seed of the same parent plant, (a condition likely to be encountered in many epiphyte or terrestrial bromeliad species) will outcross but this will occur between sibs or half-sib individuals with limited genetic variability generated. On the other hand, self-compatible plants which occur in large populations, and which engage in mixed mating, may generate reasonable levels of heterozygosity.

The prevalence of the 'steady state' type flowering phenology in most species of diverse genera of bromeliads, as demonstrated in this study, coupled with the marked protandry found in many species, will both tend to promote mixed mating, since the limited number of flowers (sometimes just one or two opened each day) will ensure that the vector will move from plant to plant, whilst the protandry, which occurs in many of these species, which eventually converts into an approach herkogamy form, means that the hummingbird vectors are likely to contact the stigma on first approach the flower. Thus, many of these self-compatible Vriesea and other taxa are likely to have levels of outcrossing with a mixed self- and cross-pollination situation. Several species in which post-pollination events were studied by mean of fluorescence microscopy for daily intervals post-pollination also evinced a more rapid cross-pollen tube growth in the style at 24 hours, and an elevated incidence of ovule penetrations in the 48-96h period, in crossed vis-a-vis selfed pistils. Such pollen competition in natural pollination conditions, where mixed self- and cross- pollen loading on the stigma may occur, may well lead to enhanced cross-fertilized ovules simply because cross-pollen tubes may reach the ovules ahead of self-pollen tubes.

6.4. CONCLUSION

In conclusion, the bromeliads of the Atlantic Rainforest of SE Brazil present a rather enigmatic evolutionary situation. Although they show a high level of taxonomic diversity and endemism ('biodiversity'), they mostly have a relatively uniform pollination service from hummingbirds and they are mostly lacking in genetic self-incompatibility mechanisms. Two factors which may produce levels of genetic heterozygosity in bromeliad populations are the 'steady state' or 'traplining' type of flowering phenology, whereby the few flowers available per plant per day keep the pollinator moving (and transfering pollen) between plants; and also the quite prevalent protandry, in which the stigma, although initially located between the anthers (and non-receptive at this stage), subsequently, via elongation of the style, becomes exserted beyond the anthers to give a condition of approach herkogamy. This situation means that a vector on approaching a flower bearing pollen, is likely to contact the stigma first. Another phenomenon which might enhance cross-pollination in some species is differential growth rates between self- versus cross-pollen in the style and ovary. To what extent this situation prevails will need to be stablished by careful monitoring of pollen tube growth in larger samples of hand-pollinated pistils.

It is interesting to compare this situation encountered with Bromeliaceae with other groups of herbaceous tropical forest monocotyledons e.g. the Orchidaceae, Araceae, Zingiberaceae and Heliconiaceae.

In this context, the orchids are a closer analogy since they also have epiphytic and terrestrial species, and show high levels of taxonomic diversity, and endemicity. A striking difference between the orchids and bromeliads is that many species of orchids show considerable complexity of floral biology and pollinator interaction. Thus, specialization in this group often seems to be associated with specialized pollinator service and it is notable that hymenopterous vectors (particularly euglossine bees) are prevalent in this group rather than hummingbirds. Also in this family, deceit pollination, involving mimicry of food site or sexual mimicry ('pseudo-copulation') occur (Pijl & Dodson, 1966; Ackerman, 1988). Also self-incompatibility is known in a number of orchids groups (Richards, 1986) although very few Atlantic Rainforest species have been studied from this point of view.

In the Zingiberales, Heliconia species show some similarities with the bromeliads in that they are often hummingbird pollinated (often with red floral bracts) and show traplining phenology, and also seem to lack genetic self-incompatibility (Kress, 1983).

Indeed, Ackerman (1986), in a review, of pollination strategies in epiphytic species, has contrasted traplining taxa, which include the Bromeliaceae, Cactaceae, Gesneriaceae and Heliconiaceae, which hummingbird or bat, large bee or hawkmoth pollination prevail, with the Orchidaceae in which traplining is rare, but in which complex hymenoptera pollination is the rule. Since, as Ackerman (1986) pointed out, the epiphytic habit involves a number of common constraints e.g. populations consisting of small plants, scattered in 'hyper-dispersed cluster', these two broad pollination strategies, traplining with large pollinator vectors, or complex pollination biology involving small hymenoptera, seem to be alternative adaptative strategies adopted by these herbaceous groups (epiphytic and terrestrial taxa) of the tropical forest. Given the taxonomic diversity and endemicity shown by both the Bromeliaceae and Orchidaceae, both strategies seem to be equally successful solutions.

CHAPTER 7. REFERENCES

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APPENDIX 1. Taxa of Bromeliaceae of the Atlantic Rainforest province.

TAXA	SOUTHEASTERN SECTOR							EASTERN SECTOR				SOUTHERN SECTOR							NORTHEASTERN SECTOR				
	RES	MAN	GRA	LWF	MWF	HIG	MES	RES	MAN	LWF	MES	RES	MAN	LWF	MWF	HIG	AF	MES	RES	MAN	LWF	MWF	MES
Acanthostachys strobilaceae	x			x				x		x		x		x									
Aechmea alopecurus**					x																		
Aechmea ampla**								x															
_Aechmea apocalyptica_*															x		x						
Aechmea aquilega v. aquilega								x											x				
Aechmea araneosa**					x																		
Aechmea azurea**				x																			
Aechmea bambusoides**							x																
Aechmea bicolor**														x									
Aechmea blanchetiana**										x													
Aechmea blumenavii**															x								
Aechmea bocainensis**				x																			
Aechmea brachycaulis										x											x		
Aechmea bromellifolia	x							x										x					
Aechmea caesia**					x																		
Aechmea calyculata**														x									
Aechmea candida**														x									
_Aechmea capitata_*																							
Aechmea cariocae**				x																			
Aechmea castanea**				x																			
Aechmea caudata v. caudata	x			x								x		x									
Aechmea chlorophylla				x				x															
Aechmea coelestis v. acutifolia**				x																			
Aechmea coelestis v. coelestis	x			x								x											

Appendix 1. Continued

*Aechmea conifera***										x													
*Aechmea cylindrata**														x	x								
*Aechmea dealbata***				x																			
*Aechmea depressa***										x													
*Aechmea digitata***										x													
*Aechmea distichantha v. distichantha f. albiflora***															x								
Aechmea distichantha v. distichantha f. distichantha	x			x	x							x		x	x								
Aechmea distichantha v. glaziovii					x										x								
Aechmea distichantha v. schlumbergeri							x																
*Aechmea distichnatha v. vernicosa***				x																			
*Aechmea eurycorymbus***																					x		
*Aechmea fasciata v. fasciata***				x																			
*Aechmea fasciata v. flavo-vittata***				x																			
*Aechmea fasciata v. pruinosa***				x																			
*Aechmea fasciata v. purpurea***				x																			
*Aechmea fosteriana***										x													
*Aechmea fulgens v. fulgens***																					x		
*Aechmea gamosepala v. gamosepala**												x		x									
*Aechmea gamosepala v. nivea***												x											
Aechmea gracilis			x	x										x	x								
*Aechmea guaratubensis***												x											
*Aechmea hostilis***				x																			
*Aechmea kerteziae***												x											
*Aechmea kleinii***															x								

Appendix 1. Continued

Aechmea lamarchei	x							x			x												
*Aechmea lindenii v. lindenii***														x									
*Aechmea lingulata v. froesii***								x															
Aechmea lingulata v. lingulata	x							x										x					
*Aechmea lingulata v. patentissima***								x															
*Aechmea macrochlamys***				x																			
Aechmea mertensii										x													
*Aechmea miniata v. miniata***										x													
*Aechmea mollis***								x															
*Aechmea mulfordii***																			x				
Aechmea multiflora				x						x													
*Aechmea muricata***																			x				
*Aechmea nervata***	x																						
*Aechmea nudicaulis v. aequalis***				x																			
Aechmea nudicaulis v. aureo-rosea	x		x	x	x	x																	
*Aechmea nudicaulis v. plurifolia***	x																						
Aechmea nudicaulis var. cuspidata	x	x	x	x	x	x	x																
Aechmea organensis			x	x										x	x								
*Aechmea orlandiana***				x																			
*Aechmea ornata v. hoehneana**														x	x								
*Aechmea ornata v. nationalis***														x									
*Aechmea ornata v. ornata**														x	x								
Aechmea pectinata				x	x									x	x								
Aechmea perforata	x							x															
Aechmea phanerophlebia							x																

Appendix 1. Continued

*Aechmea pimenti-velosoi v. glabra***												x											
*Aechmea pimenti-velosoi v. pimenti-velosoi***												x											
*Aechmea pineliana v. minuta***					x																		
*Aechmea pineliana v. pineliana**				x	x																		
*Aechmea pitcairnioides***								x															
*Aechmea podantha***				x																			
*Aechmea prava***					x																		
*Aechmea purpureo-rosea***				x																			
*Aechmea racinae v. erecta***				x																			
*Aechmea racinae v. racinae***				x																			
*Aechmea racinae v. tubiformis***				x																			
*Aechmea ramosa v. festiva***				x																			
*Aechmea ramosa v. ramosa***				x																			
*Aechmea recurvata v. benrathii***														x									
*Aechmea recurvata v. ortgiesii**														x	x								
*Aechmea recurvata v. recurvata**												x		x									
*Aechmea roberto-anselmii***				x																			
*Aechmea saxicola***			x																				
*Aechmea sphaerocephala***	x																						
Aechmea squarrosa				x																			
*Aechmea stelligera***																						x	
*Aechmea tomentosa***																						x	
*Aechmea triangularis***				x																			
*Aechmea triticina v. capensis**	x						x																
*Aechmea triticina v. triticina***				x																			
*Aechmea turbinocalyx***								x															
*Aechmea vanhoutteana***					x																		

Appendix 1. Continued

*Aechmea victoriana v. discolor***	x																						
*Aechmea victoriana v. victoriana***				x																			
*Aechmea warasii***				x																			
*Aechmea weilbachii v. pendula***				x																			
*Aechmea weilbachii v. weilbachii***				x																			
*Aechmea werdermannii***																						x	
*Aechmea winklerii***														x									
*Aechmea wittmackiana***																		x					
Ananas ananassoides	x						x																
Ananas bracteatus v. bracteatus	x											x											
*Araeococcus parviflorus***										x													
*Billbergia alfonsi-joannis***														x									
*Billbergia amoena v. stolonifera f. stolonifera***	x																						
*Billbergia amoena v. stolonifera f. viridiflora***	x																						
*Billbergia amoena v. viridis**	x			x																			
Billbergia amoena var. amoena	x			x	x	x		x		x	x												
Billbergia amoena var. minor										x													
Billbergia amoena var. rubra	x					x																	
*Billbergia bradeana***					x																		
Billbergia brasiliensis					x									x									
*Billbergia chlorantha***					x																		
*Billbergia chlorosticta***										x													
*Billbergia cylindrostachya***				x																			
*Billbergia debilis***								x															
Billbergia distachia v. concolor				x										x									

Appendix 1. Continued

Billbergia distachia v. distachia			x	x	x							x		x	x								
*Billbergia distachia v. maculata***														x									
*Billbergia distachia v. straussiana**												x											
Billbergia elegans							x																
Billbergia euphemiae v. euphemiae				x						x													
*Billbergia euphemiae v. nudiflora***				x																			
*Billbergia euphemiae v. purpurea***							x																
*Billbergia horrida v. horrida**				x																			
*Billbergia iridifolia v. concolor***	x																						
Billbergia iridifolia v. iridifolia				x						x													
*Billbergia laxiflora***				x																			
*Billbergia leptopoda***							x																
*Billbergia lymanii v. angustifolia***				x																			
*Billbergia lymanii v. lymanii***				x																			
*Billbergia macrantha***				x																			
*Billbergia minarum***							x																
Billbergia morelii				x																		x	
Billbergia nutans v. nutans															x								
*Billbergia nutans v. schimperiana***														x									
*Billbergia pyramidalis v. lutea***	x																						
*Billbergia pyramidalis v. vernicosa***				x																			

Appendix 1. (Cont.)

Billbergia pyramidalis v.pyramidalis	x		x	x																		
*Billbergia reichardtii***							x															
Billbergia sanderiana					x																	
*Billbergia seidelii***				x																		
*Billbergia tweediana v. latisepala***	x																					
*Billbergia tweediana v. minor***				x																		
*Billbergia tweediana v. tweediana**	x		x																			
*Billbergia vittata**				x	x																	
Billbergia zebrina	x			x								x		x								
Bromelia antiachantha	x											x										
*Bromelia balansae***								x														
Bromelia binotii	x							x														
Bromelia laciniosa	x																					
Bromelia lagopus			x	x																		
*Canistrum aurantiacum***																					x	
Canistrum cyathiforme				x	x									x	x							
*Canistrum fosterianum***										x												
*Canistrum giganteum***					x																	
Canistrum lindenii v. lindenii f. procerum				x										x								
*Canistrum lindenii v. lindenii f. parvum***														x								
*Canistrum lindenii v. lindenii f. elatum***														x								
*Canistrum lindenii v. lindenii f. humile***														x								

Appendix 1. (Cont.)

*Canistrum lindenii v. lindenii f. lindenii***														x									
Canistrum lindenii v. lindenii f. magnum				x										x									
*Canistrum perplexum***															x								
*Canistrum triangulare***					x																		
Catopsis berteroniana	x			x				x		x		x											
Catopsis sessiliflora				x						x		x		x									
*Cryptanthus acaulis v. acaulis***	x																						
*Cryptanthus acaulis v. argenteus***	x																						
*Cryptanthus beuckeri***										x													
*Cryptanthus bromelioides v. bromelioides***				x																			
*Cryptanthus fosterianus***																					x		
*Cryptanthus incrassatus***	x																						
*Cryptanthus marginatus***				x																			
*Cryptanthus maritimus***	x																						
*Cryptanthus pickelii***																					x		
*Cryptanthus praetextus***				x																			
*Cryptanthus pseudopetiolatus***										x													
*Cryptanthus pseudoscaposus***					x																		
Cryptanthus schwackeanus							x																
*Cryptanthus sinuosus***	x																						
*Cryptanthus zonatus f. zonatus***																					x		
*Cryptanthus zuthae***								x															
*Dyckia brevifolia***																		x					

Appendix 1. (Cont.)

Dyckia cabrerae**																		x					
Dyckia choristaminea**																		x					
Dyckia commixta																		x					
Dyckia crocea**																		x					
Dyckia deltoidea**																x							
Dyckia distachya																		x					
Dyckia dusenii**																x							
Dyckia encholirioides v. encholirioides**												x											
Dyckia encholirioides v. rubra**												x											
Dyckia fosteriana var. fosteriana**																x							
Dyckia fosteriana var. robustior**																x							
_Dyckia frigida_*												x						x					
Dyckia hatschbachii**												x											
Dyckia hebdyngii**												x											
Dyckia ibiramensis**												x											
Dyckia irmgardiae**												x											
Dyckia leptostachya												x				x							
Dyckia maritima**												x											
Dyckia microcalyx v. microcalyx																		x					
Dyckia monticola**																		x					
Dyckia pectinata**							x																
Dyckia pernambucana**																							x
Dyckia pseudococcinea	x											x											
Dyckia reitzii**																x							
Dyckia remotiflora v. montevidensis												x											
Dyckia remotiflora v. remotiflora												x											
Dyckia selloa**																x							

Appendix 1. (Cont.)

*Encholirium gracile***											x												
*Encholirium horridum***								x															
*Fernseea bocainensis***					x																		
*Fernseea itatiaiae***						x																	
Guzmania lingulata var. minor														x									
Hohembergia augustae				x										x									
*Hohembergia belemii***											x												
Hohembergia blanchetii				x						x													
*Hohembergia brachycephala***										x													
*Hohembergia castelnosii***								x															
*Hohembergia disjuncta***										x													
*Hohembergia littoralis***										x													
*Hohembergia membranostrobilus***			x																				
*Hohembergia minor***								x															
*Hohembergia pabstii***								x															
Hohembergia ramageana				x						x											x	x	
*Hohembergia ridleyi***																					x		
Hohembergia rosea	x									x													
*Hohembergia salzmanii***								x															
*Neoregelia abendrothae***					x																		
*Neoregelia albiflora***					x																		
*Neoregelia ampullacea***				x																			
*Neoregelia angustifolia***					x																		
*Neoregelia binotii***				x																			
*Neoregelia brevifolia***					x																		
*Neoregelia camoriniana***				x																			

Appendix 1. (Cont.)

*Neoregelia carcharodon v. atroviolacea***				x																			
*Neoregelia carcharodon v. carcharodon**				x	x																		
*Neoregelia carolinea v. carolinea**				x	x																		
Neoregelia chlorosticta					x									x									
*Neoregelia compacta***	x																						
*Neoregelia concentrica***				x																			
Neoregelia coriacea				x																			
*Neoregelia correia-araujii***				x																			
*Neoregelia cruenta**	x	x	x																				
*Neoregelia cyanea***							x																
*Neoregelia diversifolia***				x																			
*Neoregelia doeringiana***				x																			
*Neoregelia dungsiana***					x																		
*Neoregelia eltoniana***	x																						
*Neoregelia fluminenesis***					x																		
*Neoregelia formosa**				x	x																		
*Neoregelia fosteriana***					x																		
*Neoregelia gavionensis***				x																			
*Neoregelia hoehneana***				x																			
*Neoregelia indecora**	x			x																			
*Neoregelia johannis***	x																						
*Neoregelia kautskyi***					x																		
*Neoregelia kuhlmannii***				x																			
Neoregelia laevis	x										x												
*Neoregelia lilliputiana***					x																		
*Neoregelia lymaniana***					x																		
*Neoregelia macahensis***					x																		
*Neoregelia macrosepala***					x																		

Appendix 1. (Cont.)

*Neoregelia maculata***	x																						
*Neoregelia macwilliamsii***	x																						
*Neoregelia magdalenae v. magdalenae***					x																		
*Neoregelia magdalenae var. teresae***					x																		
*Neoregelia marcelii***				x																			
*Neoregelia marmorata***	x																						
*Neoregelia martinellii***										x													
*Neoregelia melanodonta***	x																						
*Neoregelia oligantha***							x																
*Neoregelia pascoalina***										x													
*Neoregelia pauciflora***					x																		
*Neoregelia paulistana***	x																						
*Neoregelia pineliana v. pineliana***					x																		
*Neoregelia punctatissima***					x																		
*Neoregelia rubrifolia***					x																		
*Neoregelia sapiatibensis***	x																						
*Neoregelia sarmentosa**	x			x																			
*Neoregelia seideliana***					x																		
*Neoregelia simulans***					x																		
*Neoregelia spectabilis***				x																			
*Neoregelia tigrina***					x																		
*Neoregelia tristis***					x																		
*Neoregelia wilsoniana***										x													
*Neoregelia zonata***	x																						
*Nidularium angresis***				x																			
*Nidularium antoineanum***					x																		

Appendix 1. (Cont.)

*Nidularium apiculatum v. serrulatum***				x																			
*Nidularium apiculatum v. apiculatum***					x																		
*Nidularium atalaiensis***				x																			
*Nidularium billbergioides f. azureum**	x			x																			
Nidularium billbergioides v. billbergioides	x			x	x					x		x		x									
*Nidularium burchellii***				x																			
*Nidularium correia-araujii***				x																			
*Nidularium ferdinando-coburgii***					x																		
*Nidularium fulgens***					x																		
Nidularium innocentii v. innocentii	x			x								x		x									
*Nidularium innocentii v. paxianum***														x									
*Nidularium innocentii v. wittmackianum***														x									
*Nidularium insularis***	x																						
*Nidularium itatiaiae***					x																		
*Nidularium longiflorum***					x																		
*Nidularium microps f. acuminatum***				x																			
*Nidularium microps f. bicense***				x																			
*Nidularium microps f. elata***				x																			
*Nidularium microps f. microps***				x																			
*Nidularium microps f. pallidum***				x																			
*Nidularium pedicellatum***				x																			

Appendix 1. (Cont.)

*Nidularium procerum v. kermesianum***														x									
Nidularium procerum v. procerum				x	x									x	x								
*Nidularium pulcherrimum***				x																			
*Nidularium purpureum v. albiflorum***				x																			
Nidularium purpureum v. purpureum				x										x									
*Nidularium regelioides***				x																			
Nidularium rosulatum	x											x											
*Nidularium rubens***				x																			
*Nidularium rutilans***					x																		
Nidularium scheremetiewii				x	x									x									
*Nidularium seidelii**	x			x																			
*Nidularium simulans***				x																			
*Nidularium terminale***				x																			
*Nidularium utriculosum***	x																						
*Nidularium viridium***				x																			
*Orthophytum duartei***							x																
*Orthophytum foliosum***							x																
*Orthophytum fosterianum***					x																		
*Orthophytum sanctum***					x																		
*Orthophytum vagans***						x																	
*Pitcairnia albiflos***			x																				
*Pitcairnia beycalema***					x																		
*Pitcairnia burle-marxii***						x																	
*Pitcairnia carinata***						x																	
*Pitcairnia decidua***						x																	

Appendix 1. (Cont.)

*Pitcairnia encholirioides***						x																	
Pitcairnia flammea v. *corcovadensis***				x																			
Pitcairnia flammea v. *flammea**	x		x	x	x	x																	
Pitcairnia flammea v. *floccosa*					x	x									x	x							
Pitcairnia flammea v. *glabrior*					x	x										x							
Pitcairnia flammea v. *macropoda***							x																
Pitcairnia flammea v. *pallida***					x																		
Pitcairnia flammea v. *roezlii**			x	x																			
Pitcairnia lancifolia v. *lancifolia***					x																		
Pitcairnia lancifolia v. *minor***					x																		
*Pitcairnia pumila***					x																		
*Pitcairnia staminea***			x																				
*Pitcairnia suaveolens***				x																			
*Portea filifera***							x																
*Portea fosteriana***										x													
*Portea kermesina***								x															
*Portea leptantha***																						x	
Portea petropolitana v. *extensa***	x																						
Portea petropolitana v. *noettigii**	x						x																
Portea petropolitana v. *petropolitana***	x																						
*Portea pickelii***																						x	
Portea silveirae							x	x															
Pseudoananas sagenarius	x			x			x			x		x											

Appendix 1. (Cont.)

*Quesnelia arvensis***	x																						
*Quesnelia augusto-coburgii***					x																		
*Quesnelia blanda**				x			x																
*Quesnelia edmundoi v. edmundoi***				x																			
*Quesnelia edmundoi v. intermedia***				x																			
*Quesnelia edmundoi var. rubro-bracteata***				x																			
*Quesnelia humilis***															x								
*Quesnelia imbricata**														x	x								
*Quesnelia indecora***							x																
*Quesnelia lateralis***					x																		
*Quesnelia liboniana**				x	x																		
*Quesnelia marmorata**	x	x		x																			
*Quesnelia quesneliana**	x			x																			
*Quesnelia seideliana***				x																			
*Quesnelia testudo***	x																						
*Streptocalyx curranii***										x													
*Streptocalyx floribundus**	x			x																			
*Streptocalyx lanatus***										x													
Tillandsia aeranthos												x		x									
Tillandsia aeris-incola				x	x										x								
*Tillandsia araujei v. araujei***			x																				
*Tillandsia araujei v. minima***			x																				
*Tillandsia brachyphylla***			x																				
Tillandsia bulbosa										x													
*Tillandsia carminea***						x																	
Tillandsia crocata					x							x						x					

Appendix 1. (Cont.)

Tillandsia dura	x		x									x											
*Tillandsia gardneri v. rupicola***			x																				
*Tillandsia gardneri v. virescens***	x																						
Tillandsia garneri v. gardneri	x	x	x	x	x	x					x	x						x					x
Tillandsia geminiflora v. geminiflora	x			x	x	x	x					x		x				x					
*Tillandsia geminiflora v. incana***				x																			
*Tillandsia globosa v. alba***				x																			
Tillandsia globosa v. globosa				x	x																		
*Tillandsia globosa v. major***				x																			
*Tillandsia grazielae***						x																	
*Tillandsia kautskyi***				x																			
Tillandsia linearis					x													x					
Tillandsia lorentziana																		x					
Tillandsia mallemontii	x					x						x						x					
*Tillandsia montana**																x	x						
*Tillandsia nuptialis***						x																	
Tillandsia polystachia						x											x						
*Tillandsia reclinata***						x																	
Tillandsia recurvata				x										x				x					
*Tillandsia rosea**			x			x																	
*Tillandsia segregata***				x																			
Tillandsia spiculosa v. ustulata				x	x									x	x								
*Tillandsia sprengeliana***			x																				
Tillandsia streptocarpa																		x					
*Tillandsia stricta v. disticha***																		x					
Tillandsia stricta v. stricta	x	x	x	x	x	x	x	x		x		x		x	x	x	x	x					
*Tillandsia sucrei***			x																				
*Tillandsia tenuifolia v. disticha**					x	x																	

Appendix 1. (Cont.)

*Tillandsia tenuifolia v. dungsiana***			x																				
*Tillandsia tenuifolia v. saxicola**			x			x																	
Tillandsia tenuifolia v. surinamensis	x		x	x	x					x		x		x	x							x	
Tillandsia tenuifolia v. tenuifolia	x			x	x	x	x			x	x	x		x							x		
Tillandsia tricholepis v. tricholepis	x			x	x		x					x						x					
Tillandsia usneoides	x	x		x	x		x	x	x	x	x	x	x	x	x		x	x	x		x	x	x
*Vriesea agostiniana***				x																			
*Vriesea altimontana***						x																	
Vriesea altodaserrae				x	x									x	x								
*Vriesea amethistina***					x																		
*Vriesea appariciana***						x																	
*Vriesea atra v. atra***						x																	
*Vriesea atra v. variegata***						x																	
*Vriesea atrococcinea***				x																			
*Vriesea barilletii***					x																		
*Vriesea biguassuensis***														x									
*Vriesea billbergioides v. billbergioides**					x	x																	
*Vriesea billbergioides v. subnuda***					x																		
*Vriesea bituminosa v. bituminosa**					x	x																	
*Vriesea bleheri v. atroviolacea***				x																			
*Vriesea bleheri v. bleheri***				x																			
Vriesea brasiliana *			x			x																	
*Vriesea brassicoides***			x																				

Appendix 1. (Cont.)

*Vriesea brusquensis***													x										
*Vriesea cacuminis***						x																	
Vriesea carinata				x	x					x				x	x								
Vriesea corcovadensis			x	x	x									x									
*Vriesea correia-araujei***				x																			
Vriesea crassa						x																	
*Vriesea delicatula***				x																			
Vriesea drepanocarpa					x										x								
Vriesea duvaliana				x						x													
*Vriesea eltoniana***				x																			
*Vriesea ensiformis v. bicolor**				x	x																		
Vriesea ensiformis v. ensiformis	x			x	x		x			x		x		x	x								
*Vriesea ensiformis v. striata***														x									
Vriesea erythrodactylon v. erythrodactylon					x									x	x								
*Vriesea erythrodactylon v. rubropunctata***				x																			
*Vriesea extensa**			x			x																	
*Vriesea farneyi***						x																	
*Vriesea fenestralis**				x	x																		
Vriesea flammea	x		x	x								x		x									
*Vriesea fluminensis***						x																	
*Vriesea fosteriana***						x																	
Vriesea friburgensis v. friburgensis				x	x									x									
*Vriesea friburgensis v. paludosa**												x		x	x								
*Vriesea friburgensis v. tucumanensis**														x	x								
*Vriesea funebris***				x																			
*Vriesea geniculata**			x			x																	

Appendix 1. (Cont.)

Vriesea gigantea	x	x		x								x		x								
*Vriesea goniorachis***			x																			
*Vriesea gradata v. bicolor***				x																		
Vriesea gradata v. gradata	x			x	x																	
*Vriesea guttata v. eguttata***															x							
Vriesea guttata v. guttata				x	x										x							
*Vriesea guttata v. striata***														x								
*Vriesea haematina***					x																	
Vriesea heterostachys				x	x									x								
Vriesea hieroglyphica v. hieroglyphica				x	x									x								
*Vriesea hieroglyphica v. zebrina***					x																	
*Vriesea hoehneana***						x																
*Vriesea hydrophora***					x																	
*Vriesea imperialis***						x																
Vriesea incurvata				x	x									x								
Vriesea inflata				x	x									x								
*Vriesea interrogatoria***					x																	
*Vriesea itatiaiae***					x																	
Vriesea jonghei				x	x																x		
*Vriesea joyae v. parvula***				x																			
*Vriesea joyae var. joyae***				x																			
*Vriesea languida***					x																	
*Vriesea leptantha***					x																	
*Vriesea lidicensis***				x																			
Vriesea longicaulis					x										x								
*Vriesea longiscapa**	x				x																		
Vriesea lubbersii			x	x										x	x								
*Vriesea modesta**				x	x																		
Vriesea x morreniana				x	x									x	x								

Appendix 1. (Cont.)

*Vriesea morrenii***					x																		
*Vriesea muelleri***														x									
Vriesea neoglutinosa	x											x											
*Vriesea noblickii***											x												
*Vriesea pabstii***					x																		
*Vriesea pallidiflora***					x																		
*Vriesea paraibica***					x																		
*Vriesea paratiensis***				x																			
*Vriesea pardalina**					x		x																
*Vriesea parviflora***					x																		
*Vriesea pastuchoffiana***					x																		
*Vriesea pauciflora***				x																			
*Vriesea pauperrima***				x																			
*Vriesea penduliflora***					x																		
*Vriesea pereirae***					x																		
Vriesea phillipocoburgii				x	x	x						x		x	x	x	x						
*Vriesea pinotii***												x											
*Vriesea platynema v. flava***																x							
Vriesea platynema v. platynema	x			x	x	x								x	x								
*Vriesea platynema v. striata***														x									
*Vriesea platynema v. variegata***														x									
*Vriesea platzmanii***												x											
*Vriesea poenulata**				x	x																		
Vriesea procera v. debilis				x	x					x		x											
Vriesea procera v. procera	x			x				x		x		x										x	
Vriesea procera v. rubra				x				x		x													
Vriesea procera v. tenuis	x				x									x									
Vriesea psittacina v. decolor														x									
Vriesea psittacina v. psittacina				x	x					x													
*Vriesea psittacina v. rubrobracteata***				x																			

Appendix 1. (Cont.)

*Vriesea punctulata***				x																			
*Vriesea racinae***					x																		
Vriesea recurvata				x						x													
*Vriesea regina**			x			x																	
*Vriesea rhodostachys***					x																		
Vriesea rodigasiana	x			x						x				x									
*Vriesea rubyae***					x																		
*Vriesea ruschii***					x																		
*Vriesea saundersii***			x																				
Vriesea scalaris v. scalaris				x	x									x	x								
*Vriesea sceptrum v. sceptrum f. flavobracteata***				x																			
*Vriesea sceptrum v. sceptrum***					x																		
*Vriesea serrana***					x																		
Vriesea simplex				x	x					x													
*Vriesea sparsiflora v. breviscapa***					x																		
*Vriesea sparsiflora v. sparsiflora***					x																		
*Vriesea sucrei***	x																						
*Vriesea taritubensis v. brevisepala**				x																			
*Vriesea taritubensis v. taritubensis***				x																			
*Vriesea thyrsoidea***						x																	
*Vriesea tijucana***				x																			
*Vriesea triangularis***														x									
*Vriesea triligulata***					x																		
Vriesea unilateralis				x	x									x	x								
Vriesea vagans					x									x	x								
*Vriesea vidalii***					x																		

Appendix 1. (Cont.)

*Vriesea vinicolor***						x																	
*Vriesea vulpinoideae***														x									
*Vriesea wawranea***					x																		
*Wittrockia bragarum***						x																	
*Wittrockia campos-portoi v. campos-portoi***				x																			
*Wittrockia campos-portoi v. robusta***				x																			
*Wittrockia minuta***															x								
*Wittrockia smithii***															x								
Wittrockia superba	x			x								x		x									

* Indicates endemism for sector of the Atlantic Rainforest province.

** Indicates narrow endemism for type of vegetation and sector.

Source: Smith & Downs (1974, 1977, 1979); Luther & Sieef, 1992; personal observation.