PHYLOGENETIC AND ONTOGENETIC INFLUENCES ON THE DISTRIBUTION OF ANTHOCYANINS AND BETACYANINS IN LEAVES OF TROPICAL PLANTS

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We examined the anatomy of expanding, mature, and senescing leaves of tropical plants for the presence of red pigments: anthocyanins and betacyanins. We studied 463 species in total, 370 genera, belonging to 94 families. This included 21 species from five families in the Caryophyllales, where betacyanins are the basis for red color. We also included 14 species of ferns and gymnosperms in seven families and 29 species with undersurface coloration at maturity. We analyzed 399 angiosperm species (74 families) for factors (especially developmental and evolutionary) influencing anthocyanin production during expansion and senescence. During expansion, 44.9% produced anthocyanins and only 13.5% during senescence. At both stages, relatively few patterns of tissue distributions developed, primarily in the mesophyll, and very few taxa produced anthocyanins in dermal and ground tissue simultaneously. Of the 35 species producing anthocyanins both in development and senescence, most had similar cellular distributions. Anthocyanin distributions were identical in different developing leaves of three heteroblastic taxa. Phylogeny has influenced the distribution of anthocyanins in the epidermis and mesophyll of expanding leaves and the palisade parenchyma during senescence, although these influences are not strong. Betacyanins appear to have similar distributions in leaves of taxa within the Caryophyllales and, perhaps, similar functions. The presence of anthocyanins in the mesophyll of so many species is inconsistent with the hypothesis of protection against UV damage or fungal pathogens, and the differing tissue distributions indicate that the pigments may function in different ways, as in photoprotection and free-radical scavenging.

Keywords: anthocyanin, betacyanin, development, distribution, function, leaves, phylogenetic inertia.

Introduction

Red pigmentation occurs commonly in the vegetative organs of vascular plants. Except for the Caryophyllales (the core taxa of which produce betacyanins), this coloration is due to the accumulation of anthocyanins (fig. 1). Despite the interest in such pigmentation in flowers and fruits, partly because of commercial importance, we know little of the function and evolutionary significance of anthocyanins in vegetative organs, particularly leaves. Given the presence of these pigments in taxa predating flowering and fruiting, the original function must have been something other than the attraction of pollinators and dispersers.

Anthocyanins are widely distributed in leaves. They appear during leaf expansion, especially in tropical plants. They occur on abaxial leaf surfaces of mature leaves in understory plants of tropical and temperate forests and also in aquatic plants. Anthocyanins notably appear during senescence in a wide variety of plants, particularly in temperate deciduous forests (Hoch et al. 2001). Finally, anthocyanins are a response to stress, including nutrient deficiency, lack of moisture, and disease (Chalker-Scott 1999). Betacyanins also occur in leaves of species in the core Caryophyllales (Centrospermae; Mabberley

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1997), but we know even less of their distribution in leaf tissues.

A variety of hypotheses concerning anthocyanin function, particularly in leaves, has been raised, each with little supporting evidence (Wheldale 1916; Harborne 1988). The most widely held hypothesis is that these compounds defend tissues against damaging UV radiation (Lee and Lowry 1980), first postulated by Bünning (1947). In general, flavonoids strongly absorb in the ultraviolet, and their synthesis is induced by this radiation (Westhoff 1998). Yet, anthocyanins (flavonoid pigments) do not absorb particularly well in the UV-A (320–390 nm) and UV-B regions (285–320 nm, particularly above 300 nm in terrestrial radiation environments), unless modified by other molecules (fig. 1). Earlier, anthocyanins were held to absorb visible radiation, raise temperatures, and increase metabolic and growth rates (Smith 1909), yet subsequent research has not shown the predicted temperature increases (Lee et al. 1987; Gould et al. 1995). Anthocyanins have also been hypothesized to (1) defend against fungal attack (Coley 1989), (2) reduce herbivory through camouflage (Juniper 1993), (3) reduce cell damage by reacting with free radicals (Yamasaki 1997), and (4) reduce photodamage in the photosynthetic apparatus (Gould et al. 1995). The function of betacyanins in vegetative tissue is a complete mystery (Stafford 1994).

A shortcoming in conducting research to distinguish among these hypotheses has been our lack of comparative information about the distribution of pigmentation (of anthocyanins or
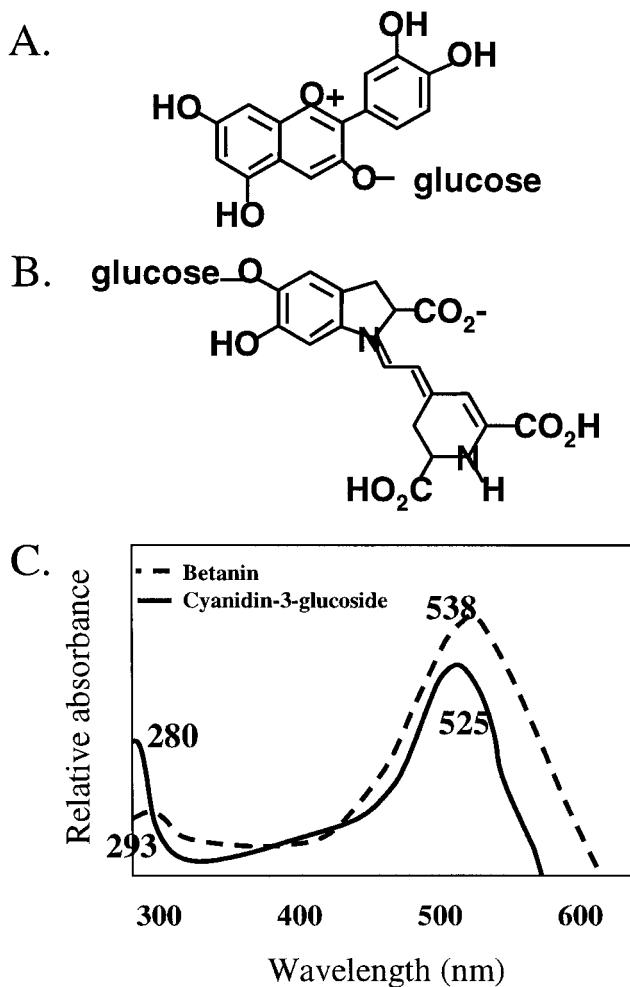
Fig. 1 Structures and absorbance spectra of red-violet pigments. *A*, An anthocyanin, cyanidin-3-glucoside. *B*, A betalain, betanin. *C*, Relative absorbance spectra for cyanidin-3-glucoside (Harborne 1967) and betanin (Strack and Wray 1994).

distribution of anthocyanins, which may be conserved within the leaf life span or at different stages in heteroblastic plants. These same constraints may also influence the distribution of betacyanins.

The purpose of this research was to analyze leaves of a large sample of tropical woody plants for the presence of anthocyanins in their leaves (as pink-violet coloration in vacuoles). Are anthocyanins particularly produced in certain tissues and at different developmental stages of leaves? Are betacyanins similarly distributed, in a much smaller sample, within the Caryophyllales? Has phylogeny influenced this pigment distribution? Are there developmental constraints, seen as few patterns of pigmentation among the many possible cell combinations or as similarities in patterns in different stages of the leaf life span? Analysis of this sample allowed us to determine the constraints of development and phylogeny on pigment distribution and to speculate on the relevance of these patterns to pigment function in leaves.

Material and Methods

We examined leaf tissues of 463 species, from 370 genera, in 94 families, primarily of plants available in the Miami area (appendix). These generally constitute a broad sample of taxa from the seasonally dry Tropics. We also added species observed at La Selva Research Station in Costa Rica (McDade et al. 1994) in April 1986 and August 1998 and Barro Colorado Island in Panama (Leigh et al. 1982) in April 1987. We observed plants at the following locations in Miami-Dade County, from January 1997 until February of 2000: (1) Fairchild Tropical Garden; (2) Gifford Arboretum, University of Miami; (3) Environmental Preserve and Campus, Florida International University; (4) Charles Deering Estate County Park; (5) Castellow Hammock County Park; (6) Ned Glen County Park; (7) residential planting, Southwest 47th Street and 59th Avenue in Miami; (8) Shark Valley, Everglades National Park; (9) the Montgomery Botanical Center; and (10) John Lloyd State Park, Broward County. From our knowledge of the local flora, we made a list of species to observe. For this list, we emphasized South Florida native plants, species common enough for multiple observations, and certain species in families poorly represented by the general collection (appendix). This list includes a few genera with many species, such as *Ficus*, but most with a moderate number.

We collected leaves from three individual plants of each taxon, examining discolored, expanding, and senescing leaves separately. We cut transverse hand sections ca. 50 μm thick with single-edge razor blades, and observed the fresh sections at ×200 with a compound light microscope. The thick hand sections and the presence of pigments in vacuoles made it possible to observe pigments in concentrations over at least three orders of magnitude. We never observed anthocyanins in discrete inclusions within vacuoles. We observed pigmentation in expanding leaves, at maturity, and during senescence. These stages in the leaf life span are under genetical/physiological control, and we consider them as developmental stages. We limited our observations of pigmentation during leaf expansion from 50% to 100% of the final lengths. We determined the presence or absence of coloration in cell vacuoles of the (1) upper epidermis; (2) hypodermis, if present; (3) palisade pa-

betacyanins), in leaf tissues, during the leaf life span, and among taxonomic groups. For instance, the function of anthocyanins in defending against damage by UV-B radiation requires their presence in the epidermis. Yet, there is some evidence of anthocyanins occurring in the mesophyll (Lee and Lowry 1980; Gould and Quinn 1999). Parkin (1918) summarized a large survey of angiosperm leaves, reporting that most produced anthocyanins in the mesophyll, but the data were not published.

A variety of factors could constrain the distribution of anthocyanins and betacyanins in leaves. Function may require pigment presence in a particular location and time to defend against UV-B radiation. Although anthocyanins are the product of a biosynthetic pathway found throughout vascular plants and bryophytes (except for the betacyanin-producing taxa in the Caryophyllales), they may not be present in certain taxa. Their distribution may be influenced by phylogeny, confounding simple correlational studies of traits and functions. Furthermore, there may be developmental constraints on the

Table 1

Presence or Absence of Anthocyanins and Betacyanins in Leaves from This Survey Showing Results for Major Taxonomic Groups, for Development, Maturity, and Senescence

Group	Number of taxa	Number in development	Number at maturity	Number in senescence
Anthocyanins:				
Angiosperms	427	179	28	53
Gymnosperms	5	0	0	0
Filicopsida	9	3	0	0
Betacyanins:				
Centrospermae	22	6	1	0
Total	463	188	29	53

renchyma; (4) spongy mesophyll; (5) bundle sheath cells only; (6) abaxial epidermis; and (7) trichomes or scales, if present. For certain analyses, we contrasted anthocyanins in cells derived from dermal tissue (1, 6, 7 above) and ground tissue (2–5 above; Sinha 1999). We used the presence of pink, red, or purple color in the vacuoles as evidence for the production of anthocyanins or betacyanins. Several reasons may make these results a slight underestimation of pigment production among individual species. It is possible that molecules may be present and not produce color in the rare conditions of high pH in the vacuole (Gould et al. 2000). We observed only plants of reproductive age; juvenile plants could produce pigments not seen at maturity. It is also possible that pigment production in a taxon may vary with geographical location.

We measured the lengths and thicknesses of the sampled leaves with a ruler and a micrometer. We also observed the same plants for the presence of anthocyanins in other organs: buds, flowers, fruits, twigs, and petioles. In some cases, we were not able to observe reproductive stages, and we consulted herbarium sheets (FTG) and regional floras.

We mapped the distribution of anthocyanins in leaf tissues at various developmental stages on a phylogeny assembled from several sources. Relationships among the major clades (family, order, and above) follow molecular phylogenies based on 18S rDNA, *rbc*L, and *atp*B (APG 1998; Soltis et al. 1999). We pruned these "backbone" trees to contain those families represented in our sample. In many cases, we were required to substitute taxa based on taxonomic affiliation at the family level. In addition, some placements are at odds with traditional classification, being based on more recent developments. For instance, we placed *Drypetes* sp. in the Humiriaceae rather than the Euphorbiaceae (appendix). We added phylogenetic structure within certain families based on additional research (Bremer et al. 1995; Cantino et al. 1997; Wagstaff and Olmstead 1997; Alverson et al. 1998, 1999; Judd et al. 1999). These refinements were added to the "backbone" phylogeny within McClade 4.0b7-19 (Maddison and Maddison 1999). A total of 399 species were represented in the final tree, referred to as the study tree. Unfortunately, many polytomies representing areas of unknown resolution remained (soft polytomies). Most of these were within families. Because these soft polytomies create difficulties for character state reconstruction (e.g., Maddison and Maddison 1992; Ackerly and Reich 1999), we used the random trees feature of MacClade 4.0 to create 100 random resolutions of the polytomous regions re-

maining in the study tree. To test for phylogenetic inertia (Maddison and Slatkin 1991) in anthocyanin distributions, we compared the distribution of the number of steps for characters on 100 random resolutions of the study tree to the number of steps on those same 100 resolutions with the character states randomly shuffled among taxa. The significance of differences between these distributions was determined by the Wilcoxon signed ranks test implemented in SYSTAT 5.2 (SPSS, Chicago). In addition, the retention index (RI) was calculated as a rough additional measure of phylogenetic inertia. When the RI = 1, homoplasy is absent and phylogenetic inertia of a character state is maximized. When the RI = 0, homoplasy is maximized and phylogenetic inertia will be low.

We also investigated developmental constraints on anthocyanin distribution in expanding plant tissues using this data set. We generated 100 data matrices by shuffling states within characters. For each randomization, we determined the number of unique combinations of anthocyanin expression and tissue type, counting how many of these combinations were dermal only, ground only, or both dermal and ground. We compared the observed proportions of anthocyanin expression to the range of values found in our randomized data sets. All files relating to phylogenetic analyses are available on request from the authors.

Results

We surveyed leaf anatomy for the presence of anthocyanins in expansion and senescence in 399 angiosperms, representing 74 families (table 1). In addition, we analyzed the leaves of 29 angiosperm species (from 19 families) with pigments noticeable from the abaxial surface throughout the life span. We also studied 14 species of gymnosperms and ferns (seven families). Within the Caryophyllales, we analyzed leaves of 21 species from five families. This is a total of 463 species from 94 families (table 1; appendix). We saw no evidence of variability of anthocyanin tissue location for the three sampled individuals in any of the species, although several species were polymorphic for the presence of anthocyanins, as *Ficus religiosa*.

Of the 399 species, 193 (48.4%) produced anthocyanins during the life span of their leaves. Thirty-five of these species produced anthocyanins during both development and senescence.

Anthocyanins in Expansion

Of the angiosperm species, 44.9% (179/399) produced anthocyanins during leaf expansion. None of the gymnosperms produced anthocyanins, even though several had discolored leaves. Three of the eight ferns surveyed produced anthocyanins (table 1). Given the seven cell layers surveyed and the possible combinations among them, a total of 127 ($2^7 - 1$ [for absence]) cell patterns were possible in the angiosperm survey. Yet, only 21 of those combinations were observed, and 88.4% of the species produced anthocyanins in only nine combinations (table 2). Anthocyanins were most commonly produced in the mesophyll, 26.3% in the palisade and spongy mesophyll and 19.0% in the palisade only. Only 24.0% of species produced anthocyanins in the epidermis.

Anthocyanins in Senescence

Among the angiosperm species, only 13.5% (54/399) produced anthocyanins at the end of the leaf life span. Of these species, we observed only 10 different cell combinations, and six of them accounted for 92.6% of all observations (table 2). Half of the species produced anthocyanins exclusively in the palisade parenchyma, while 18.5% produced anthocyanins in the palisade and spongy mesophyll. Only 9.3% of species produced anthocyanins in the epidermis.

Anthocyanins at Maturity

We sampled leaves of 29 species (from 19 families) producing anthocyanins at maturity. All of these had red-purple pigmentation visible from the undersurface. Rain forest understory herbs dominated this sample, but three taxa were aquatic plants. Of the 26 understory species, 10 produced anthocyanins in the abaxial epidermis and 10 in the spongy mesophyll. The other six species produced anthocyanins in other cell combinations. Two of the aquatic plants produced anthocyanins in the abaxial epidermis and one in the spongy mesophyll.

Betacyanins in Leaves

In our small sample of primarily woody taxa (22 species in five families) six species produced betacyanins during leaf expansion (table 1). None produced betacyanins during senescence. Four species produced anthocyanins in the adaxial epidermis, and two produced anthocyanins in the palisade and spongy mesophyll layers. One of the rain forest understory species (*Jamesbondia costaricense*, Amaranthaceae) produced betacyanins in the spongy mesophyll during its entire leaf life span.

Phylogenetic Distribution of Anthocyanins

For six of the characters, hypodermis in expanding and senescing leaves, spongy mesophyll in senescing leaves, bundle sheath cells, lower epidermis, and trichomes or scales in expanding leaves, the number of steps on 100 random resolutions of the study tree were not different from the number of steps on those trees with the states randomly shuffled within characters (table 3). In fact, these numbers were equal to the greatest number of steps possible for this character on any tree. For three other characters, parenchyma associated with vascular bundles, trichomes, and scales in expanding leaves and upper epidermis in senescing leaves, the numbers of steps on 100 random resolutions of the study tree were within one or two steps of both the number required on random shufflings and the greatest possible number of steps. Five of the characters, including epidermis, palisade parenchyma, spongy mesophyll, lower epidermis in expanding leaves, and palisade parenchyma in senescing leaves, differed significantly by four or more steps between the average number of steps in 100 random resolutions of the study tree, and the average number of steps on those same 100 trees with the character states randomly shuffled (<0.000, Wilcoxon signed ranks test; fig. 2). The retention indices for these characters were developing leaf upper epidermis, RI = 0.14; palisade parenchyma, RI = 0.25; spongy mesophyll, RI = 0.19; lower epidermis, RI = 0.16; and senescing palisade parenchyma, RI = 0.24.

Table 2

Distribution of Anthocyanins in Tissues of Developing and Senescent Leaves

UEP	HYP	PAL	SPM	VBU	LEP	TRC	Origin	Percentage in development	Percentage in senescence
—	—	*	*	—	—	—	Ground	26.3	18.5
—	—	*	—	—	—	—	Ground	19.0	50.0
—	—	—	*	—	—	—	Ground	10.6	0.0
—	—	*	—	*	—	—	Ground	3.4	0.0
—	—	—	—	*	—	—	Ground	3.4	0.0
*	—	—	—	—	*	—	Dermal	14.5	1.9
*	—	—	—	—	—	—	Dermal	9.5	7.4
*	*	*	—	—	—	—	Both	0.0	7.4
*	—	*	—	—	—	—	Both	0.6	7.4
*	*	—	—	—	—	—	Both	1.1	3.7
								88.4 (9)	96.3 (7)

Note. These combinations are the most frequent among those observed in the survey. Abbreviations include UEP = adaxial epidermis; HYP = hypodermis, if present; PAL = palisade parenchyma; SPM = spongy mesophyll; VBU = parenchyma adjacent to vascular bundles; LEP = abaxial epidermis; TRC = trichomes or scales. Asterisks symbolize the presence of anthocyanins in cell vacuoles in this tissue layer; dashes symbolize absence. Values are percentages of taxa with anthocyanins.

Table 3

Numbers of Steps Required for Anthocyanin Characters

Anthocyanin distribution characters	A	B	C
Developing leaves:			
Upper epidermis	45.6	50.7	53.0
Leaf hypodermis	9.0	9.0	9.0
Palisade parenchyma	69.3	83.0	92.0
Spongy mesophyll	56.8	65.4	70.0
Parenchyma vascular bundles	14.0	15.8	16.0
Lower epidermis	31.2	36.0	37.0
Trichomes or scales	9.0	9.9	10.0
Senescing leaves:			
Upper epidermis	14.7	14.8	15.0
Leaf hypodermis	6.0	6.0	6.0
Palisade parenchyma	36.0	45.2	47.0
Spongy mesophyll	12.0	11.9	12.0
Parenchyma vascular bundles	0.0	0.0	0.0
Lower epidermis	2.0	2.0	2.0
Trichomes or scales	0.0	0.0	0.0

Note. "A" gives the number of steps required on 100 random resolutions of the polytomies in the study tree. "B" gives the number of steps on those 100 random resolutions with the character states randomly shuffled among taxa. "C" gives the greatest number of steps possible for the character on any tree.

Discussion

The variable tissue distribution of anthocyanins and beta-cyanins in this sample of primarily tropical woody taxa suggests that a variety of factors may influence their appearance in leaves, at different developmental stages and in different tissues.

Climate

Richards (1996) commented on red leaf flush as a characteristic feature in tropical plants. The apparent correlation between the red leaf flush and the Tropics led Bünning (1947) to hypothesize that anthocyanins could protect sensitive tissue, as expanding leaves, in the harsh UV climates of equatorial latitudes. However, temperate plants may produce anthocyanins during expansion (Juniper 1993), as in the young leaves of montane plants (unpublished observations by D. W. Lee in the Cascade Mountains of Washington State, June 1999), and it is not clear how much more common the phenomenon is in tropical plants. However, red coloration in senescence is clearly uncommon in tropical plants, only 13.5% of taxa in this survey. In a survey of 91 woody taxa at Harvard Forest in Massachusetts, 70% produced anthocyanins in senescence (D. W. Lee, unpublished data). Seasonal climates (with bright and cold days during the autumn) have resulted in taxa with anthocyanins produced during senescence. A limitation of our sample (a narrow latitudinal band in the Tropics) made it impossible to look for correlations between pigmentation patterns and climate.

Undersurface coloration is not uncommon in mature leaves of understory plants in the Tropics; it also occurs in temperate understory plants, and the same is true for floating leaves of aquatic plants. Thus, with the exception of senescent coloration, climate seems not to strongly influence the distribution of anthocyanins in plants.

Morphology and Biochemistry

Almost all of the plants in this survey are woody, with a few exceptions in betacyanin-containing families and understory plants. Although we did not contrast the distribution in woody versus herbaceous plants, anthocyanins are present in expansion and senescence in many herbaceous plants (D. W. Lee, unpublished observations). Betacyanins are produced in leaves and other tissues of many herbaceous plants as well. Thus, these two growth forms may not correlate with pigment distribution.

We compared both leaf size and thickness with the presence of anthocyanins in development, hypothesizing that larger leaves may take longer to develop and may require more protection. Species with green developing leaves produced a mean leaf size of $10.7 \pm SD\ 7.5$ cm and thickness of $276 \pm SD\ 263$ μm. This was similar to a mean red leaf size of $12.1 \pm SD\ 9.1$ cm and a thickness of $263 \pm SD\ 100$ μm; these values were not significantly different from comparisons by the t-test. We did not do further tests of phylogenetic contrasts because of this lack of statistical relationship.

The species also varied in their expression of anthocyanins in reproductive and vegetative organs (besides leaves); 272/399 (68.2%) produced anthocyanins in some part of the plant other than the leaves. Ability to produce anthocyanins in other organs may influence their production in leaves; 53% of developing leaves produced anthocyanins in those species that produced anthocyanins in other structures, compared to 38% in species that were green throughout. This difference was significant ($P < 0.05$), based on 100 randomizations of two binary character states representing presence or absence of anthocyanins in leaves and anthocyanins in all other organs. This test, however, does not take the effect of phylogeny into account. The data set and numbers of character state changes were too large for simulation-based analyses of correlated character evolution such as the concentrated-changes test (Maddison and Maddison 1992).

Development

Plants produced anthocyanins during leaf expansion and senescence in specific cell layers (table 2). These patterns were identical among samples for each taxon, consistent with previous results (Lee et al. 1987; Gould and Quinn 1999), except for the remarkable variation in *Quintinia serrata* (Gould et al. 2000).

We can compare the influence of development on anthocyanin production in several ways. First, 35 species produced anthocyanins during expansion and senescence. Eight had identical tissue distributions, and 16 overlapped in pigmented tissue. The tissue distributions of only 11 of the species differed between expansion and senescence. Although there is considerable similarity between those two stages, senescent leaves more frequently produced anthocyanins in palisade tissue, even when there was a different distribution during expansion.

Three species were strongly heteroblastic in leaf morphology during development and also produced anthocyanins in their different expanding leaves. *Ficus pumila*, *Macfadyena unguis-*
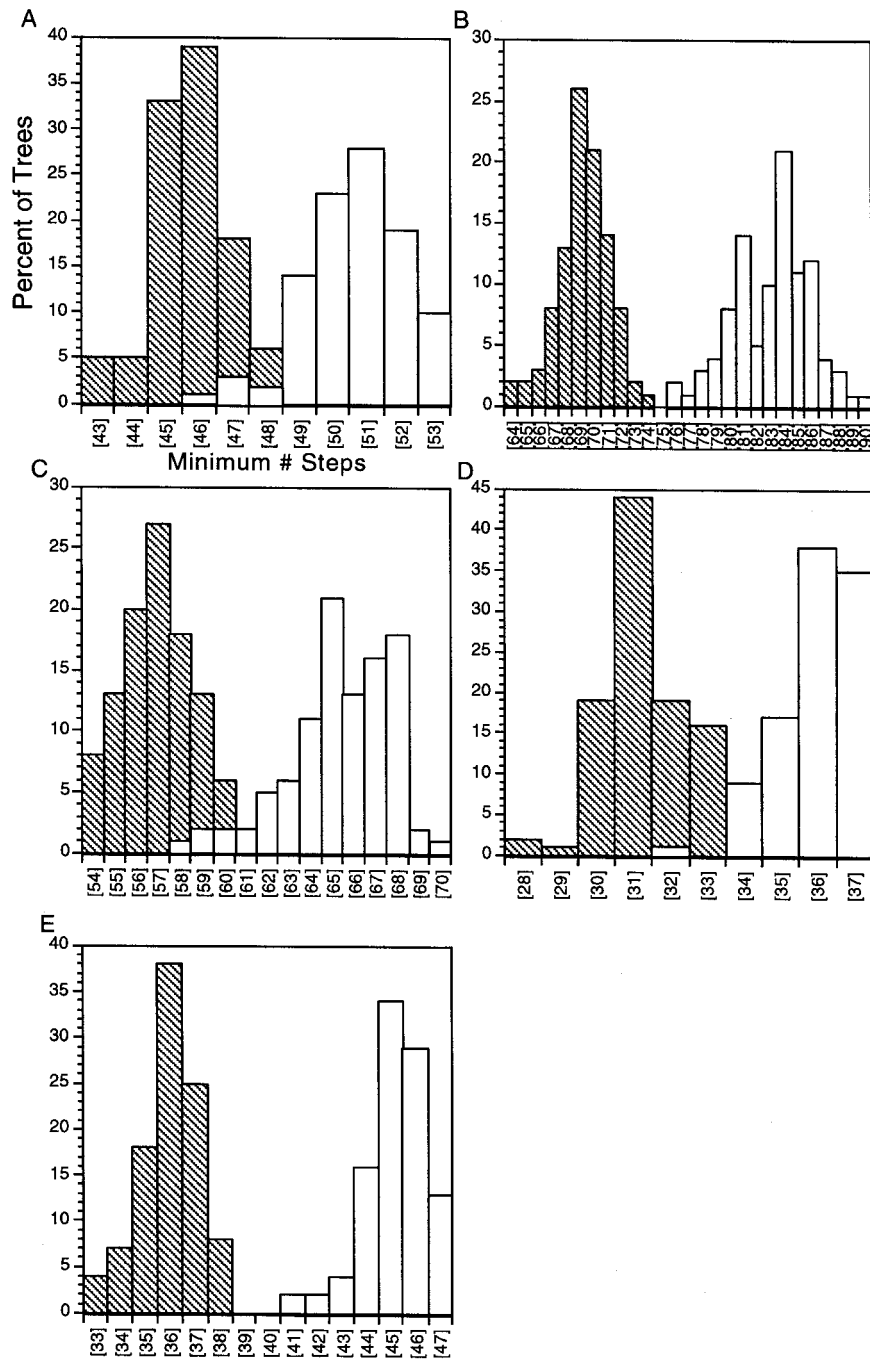
Fig. 2 A comparison of the number of steps required for characters on 100 random resolutions of the study tree, shown as hatched bars, to the number of steps required on those same 100 random resolutions with the character states randomly shuffled among taxa, shown as white bars. The number of occurrences is the number of times out of 100 that a given number of steps were required for that character. *A*, Adaxial epidermis in development. *B*, Palisade parenchyma in development. *C*, Spongy mesophyll in development. *D*, Abaxial epidermis in development. *E*, Palisade parenchyma in senescence.

cati, and *Marcgravia rectiflora* all produced dimorphic juvenile and adult stages (and *M. unguis-cati* an additional intermediate stage). Each developed a single tissue pattern of anthocyanin production.

Cell layers in leaves develop from two germ layers—dermal (L1) and ground (L2; Sinha 1999). We grouped tissue layers

into these two types, depending on their origins. We found that taxa produced anthocyanins predominantly in cell layers derived from L2 (70%) compared to L1 (30%). Surprisingly, only 6.7% of the species produced anthocyanins in cells derived from both germ layers. We found six of the seven possible combinations of anthocyanin expression limited to dermal tis-

sues and 13 of the 15 combinations limited to ground tissue. In contrast, we found only nine of the 105 combinations of both dermal and ground tissue expression of anthocyanins. The proportion of ground-only combinations was higher in our data than for any of the simulations, while the proportion of both dermal and ground combinations was lower in our data than the simulations ($P < 0.01$). These results indicate that anthocyanin expression in both dermal and ground tissues was underrepresented and ground-only combinations were overrepresented in our data set.

Thus, there is a particular developmental constraint on the distribution of anthocyanins in leaves, which helps explain the relatively few common patterns of tissue distribution. Kubo et al. (1999) described a homeobox gene (*ANL2*) that affects anthocyanin production in leaf mesophyll tissue. This is different from the *R/B* gene family and other controlling elements that specify anthocyanin production in the epidermis (Dooner et al. 1991), and there may be fundamental molecular and genetic bases for the differences in anthocyanin expression in these two tissues.

Anthocyanin synthesis in leaves was significantly correlated with their production in other plant parts. Since control of anthocyanin expression in petals and carpels (both leaflike structures) should be similar to that in leaves, such a relationship is not surprising (Fineblum and Rausher 1997).

Clearly, there are strong developmental constraints on the production of anthocyanins in leaves, as seen in the relatively few tissue combinations of anthocyanin production and in the similarities of these patterns within taxa between expanding and senescent leaves.

Phylogeny

The flavonoid pathway, which produces anthocyanins, occurs universally in all vascular plants (Shirley 1996). Anthocyanins are produced in all vascular plant groups, particularly in the angiosperms. However, in the core Caryophyllales, anthocyanins are replaced by betalain pigments (of an entirely different biosynthetic pathway), although other flavonoids are produced (Stafford 1994). The large number of genes regulating anthocyanin synthesis (Dooner et al. 1991; Holton and Cornish 1995) suggests that loss of expression may occur easily, although changes in the sites of production may be less likely. In this survey, 48 of 399 species showed no evidence of anthocyanin production. Despite the variability in expression of anthocyanins in different organs and even between closely related taxa, some broad trends were apparent in the survey. Almost all Myrtaceae produced anthocyanins in the palisade parenchyma only during leaf expansion. Anthocyanic Fabaceae produced anthocyanins in the epidermis of expanding leaves. Anthocyanins occurred in the bundle sheath cells of expanding leaves of taxa in the Malvales, with only a single exception: *Strongylodon macrobotrys*, in the Fabaceae (appendix). Anthocyanins were absent from expanding and senescing leaves in our samples from the Acanthaceae, Asteraceae, and Solanaceae and from the Asteridae in general. Most species surveyed from the Combretaceae and Lythraceae produced anthocyanins during senescence.

Although these striking distributions are consistent with phylogenetic influence, a test for overall evolutionary influence on the production of these compounds (phylogenetic inertia) should also be a statistical one, based on characters mapped on a phylogeny. In such an analysis, only five of the 14 anthocyanin characters had distributions of numbers of steps that were significantly less than random. This weak phylogenetic inertia can be seen in the similarity of distributions of the actual data set and random shufflings, which overlap or abut in several cases (fig. 2), and the low RI values reported. These results indicate that phylogenetic inertia is weak for anthocyanin distributions at the family level and above. It is possible that the polytomies present in the study tree may result in an underestimation of the degree of phylogenetic inertia. If, for each character, all polytomies are resolved so as to minimize the total number of steps for that character, retention indices increase substantially (table 4). It is possible, therefore, that further refinements of the study tree will result in an increase of phylogenetic inertia, especially within families. However, many of these resolutions are mutually contradictory among characters so that only some could realize the increases in RI indicated in table 4 with further refinement of the tree.

Function

The patterns of leaf anthocyanin production we have seen are germane to the alternative hypotheses of anthocyanin production in leaves. At the very least, the diversity of patterns is consistent with a diversity of physiological/ecological functions in plants, agreeing with the conclusions reached by Gould and Quinn (1999) in a survey of anthocyanin distribution in 25 New Zealand taxa. In general, the production of anthocyanins in the mesophyll is not consistent with the hypotheses of UV defense or pathogen defense. Interception of radiation or pathogens at the leaf surface requires production in the epidermis, although spores may enter via adaxial stomata. The predominant mesophyll distribution, always associated with at least some chlorophyll in these plants, is consistent with hypotheses of photoprotection or free radical scavenging. In senescent leaves, where a higher percentage of taxa produce anthocyanins in the palisade cell vacuoles, the pigments are well placed in relationship to the breakdown of chloroplasts, since chlorophyll degradation products are sequestered in the vacuoles (Matile et al. 1999). Any pigment distribution would be compatible with the hypotheses of temperature elevation or cam-

Table 4

Retention Indices (RI) for Characters with Significant Phylogenetic Inertia

Character	Average RI	RI maximum
Development:		
Upper epidermis	0.14	0.29
Palisade parenchyma	0.25	0.44
Spongy mesophyll	0.19	0.35
Lower epidermis	0.16	0.28
Senescence:		
Palisade parenchyma	0.24	0.41

Note. The average RI over 100 random resolutions of the study tree is compared with the RI with each polytomy resolved in order to minimize the number of steps for that character.

ouflage. Complementary evidence supporting such hypotheses will require direct experimentation.

The distribution of betacyanins in leaves was similar to anthocyanins. Both anthocyanins and betacyanins have very similar absorbance maxima of 525–540 nm, both molecules have significant antiradical activity (Yamasaki 1997; Escribano et al. 1998), and betacyanins have even less absorbance in the UV region (fig. 1). Although the sample was small, betacyanins had similar tissue distributions during development, and one understory taxon produced undersurface coloration. None of the taxa produced betacyanins during senescence, perhaps reflecting the greater metabolic cost of these nitrogenous compounds. The similar patterns suggest that the function(s) of betacyanins in leaves of taxa in the Caryophyllales may be similar to those for anthocyanins in other orders.

Conclusions

Pigment (anthocyanin and betacyanin) distribution in this broad sample of tropical taxa was not random. Leaf anthocyanins were correlated with their production in other plant organs. Their distribution was under some developmental constraints and was weakly influenced by phylogenetic background. The weak phylogenetic influence, along with the diverse tissue distributions of pigments, suggest several functions for anthocyanins and betacyanins in leaves.

Acknowledgments

Appendix

Data on Anthocyanin Distribution in the Plant Sample

For collection locations, see "Material and Methods" for more details. Key for superscripts: [1]Fairchild Tropical Garden; [2]University of Miami; [3]Florida International University; [4]residential, Dade County; [5]La Selva, Costa Rica; [6]Montgomery Foundation; [7]Shark Valley, Everglades National Park; [8]Deering Estate; [9]Ned Glen Park; [10]Barro Colorado Island, Panama; [11]Castellow Hammock; [12]John Lloyd State Park. For the anthocyanin distributions, the seven digits (1 for presence; 0 for absence) are, in order: upper epidermis, hypodermis, if present; palisade parenchyma; spongy mesophyll, parenchyma associated with vascular bundles; lower epidermis; trichomes or scales, if present. Developmental stages are indicated by leaf expansion (D), mature (M), and senescent (S). Other abbreviations are T = leaf thickness (μm); L = leaf length (cm); R = presence of anthocyanins in reproductive structures; P = presence of anthocyanins in petioles or twigs; juv. = juvenile; int. = intermediate; and ad. = adult.

ACANTHACEAE *Eranthemum pulchellum* Andr.[1] R-1, P-0,L-11,T-190; *Graptophyllum pictum* Griff.[3] R-1,P-1,L-17,T-290; *Hemigraphis alternata* (Burm. f.) T. Anderson[1] M-0001011; *Megaskapasma erythrochlamys* Lindau[1] R-1,P-0,L-24,T-180; *Pachystachys lutea*[1] Nees R-0,P-0,L-15,T-210; *Ruellia biolleyi* Lindau[5] M-0000010; *Ruellia brittonia* Leonard[1] R-1,P-1,L-19,T-330; *Thunbergia erecta* T. Anders.[1] R-1,P-0,L-3,L-210.

AMARANTHACEAE *Achyranthes aspera* L.[5] R-0,P-1; *Alternanthera maritima* (Mart.) Standl.[12] R-0,P-1; *Alternanthera sessilis* (L.) R. Br.[5] R-0,P-1; *Amaranthus hybridus* L.[3] R-0,P-1; *Cyathula achyranthoides* (HBK.) Moq.[5] R-0,P-1; *Jamesbondia costaricense* Mears *ined.*[5] M-0001010.

ANACARDIACEAE *Anacardium occidentale* L.[4] D-0011100,R-1,P-0,L-15,T-230; *Mangifera indica* L.[3] D-0001000,R-1,P-0,L-15,T-220; *Metopium toxiferum* (L.) Krug & Urb.[2] D-0010000,R-0,P-0,L-9,T-270; *Rhus copallina* L.[9] D-0011000,S-0010000,R-1,P-1,L-4,T-250; *Schinus terebinthifolius* Raddi[3] D-0001000,R-1,P-1,L-6,T-270; *Spondias purporea* L.[3] R-1,P-0,L-4,2,T-180.

ANNONACEAE *Annona glabra* L.[3] R-1,P-1,L-12,T-300; *Annona muricata* L.[6] R-0,P-0,L-11,T-220; *Annona squamosa* L.[6] R-0,P-0,L-11,T-180; *Artabotrys hexapatalus* (L. f.) Bhandari[1] R-0,P-0,L-16,T-190; *Cananga odorata* Hook. f. & Thoms.[3] R-1,P-0,L-14,T-140; *Polyalthia longifolia* Thw.[1] D-0010000,R-1,P-0,L-18,T-150; *Polyalthia suberosa* Thw.[2] D-0011000,R-1,P-0,L-5,T-170.

APOCYNACEAE *Adenium obesum* Balf.[1] D-0001000,R-1,P-1,L-8,T-490; *Allamanda cathartica* L.[1] R-1,P-1,L-11,T-510; *Alstonia scholaris* R. Br.[1] R-1,P-0,L-17,T-330; *Asclepias currasavica* L.[3] R-1,P-1,L-11,T-290; *Calotropis gigantea* (L.) R. Br. *ex* Ait.[1] R-1,P-0,L-13,T-390; *Carissa carandas* L.[3] D-0010000,S-0010000,R-1,P-1,L-3,T-500; *Catharanthus roseus* Don[1] R-1,P-1,L-4,T-270; *Cryptostegia madagascarensis* Bojer[2] R-1,P-0,L-9,T-250; *Ervatamia divaricata* (L.) Alston[1] R-1,P-0,L-14,T-399; *Kopsia fruticosa* A. DC.[1] S-0011000,R-1,P-0,L-21,T-300; *Nerium oleander* L.[4] R-1,P-0,L-17,T-480; *Ochrosia elliptica* Labill.[3] R-1,P-0,L-10,T-380; *Pachypodium lamierei* Drake[1] R-0,P-0,L-14,T-500; *Plumeria rubra* L.[1] R-1,P-0,L-27,T-300; *Sarcostemma clausa* (Jacq.) Roemer & Schultes[7] R-0,P-0,L-3,T-270; *Stephanotus floribunda* (R.Br.) Brongn.[1] R-0,P-1,L-10,T-730; *Thevetia peruviana* Schum.[1] R-0,P-0,L-11,T-260; *Trachelospermum jasminoides* Lem.[2] D-0010000,R-0,P-0,L-4,T-390; *Vallesia antillana* Woodson[2] S-0010000,R-0,P-1,L-10,T-500.

AQUIFOLIACEAE *Ilex cassine* L.[2] D-0010000,R-1,P-1,L-7,T-280; *Ilex krugiana* Loes. ex Urb.[2] D-0011000,R-1,P-0,L-6,T-250.

ARACEAE *Alocasia guttata* N. E. Brown[1] M-0001000; *Anthurium clidemioides* Standley[5] M-0001000; *Anthurium*

guyanum Bunting[1] D-1001010,R-0,P-0,L-52,T-580; *Anthurium magnificum* Hort.[1] D-0011000,R-0,P-0,L-24,T-450; *Philodendron scandens* (Aubl.) Engl.[9] M0001000; *Syngonium rayii* Croat & Grayum *ined.*[5] M-0001000; *Xanthosoma sagittifolia* (L.) Schott[3] R-0,P-0,L-50,T-300.

ARALIACEAE *Polyscias guilfoylii* Bailey[4] R-0,P-0,L-13,T-180; *Schefflera actinophylla* Harms[3] R-1,P-0,L-27,T-480; *Schefflera arboricola* Hayata[4] D-1100000,R-0,P-0,L-7,T-350; *Trevisia palmata* Vis.[1] R-0,P-0,L-45,T-310.

ARAUCARIACEAE *Agathis dammara* (Lamb.) L. G. Rich.[4] R-0,P-0,L-8,T-420.

ASTERACEAE *Baccharis angustifolia* Mich.[1] R-0,P-0,L-4,T-410; *Baccharis halimifolia* L.[1] R-0,P-1,L-4,T-320; *Borrichia arborescens* (L.) DC[1] R-0,P-0,L-5,T-1400; *Montanoa grandiflora* Hemsl.[1] R-0,P-0,L-27,T-260.
BEGONIACEAE *Begonia glabra* Aubl.[5] M-0001000; *Begonia mazae* Zeisenhenne[1] M-0000010; *Begonia pavonina* Ridl.[3] M-0001000.

BIGNONIACEAE *Amphitecna latifolia* (Mill.) Gentry[1] R-1,P-0,L-19,T-400; *Crescentia cujute* L.[1] R-1,P-1,L-14,T-230; *Dolichandrone spathacea* K. Schum.[1] D-1000010,S-0010000,R-1,P-1,L-10,T-170; *Heterophragma quadrilocare* (Roxb.) K. Schum.[3] D-0011000,R-0,P-1,L-13,T-280; *Jacaranda mimosaefolia* D. Don.[3] R-1,P-1,L-1,T-150; *Kigelia pinnata* DC.[1] D-0001000,S-0100000,R-1,P-0,L-13,T-260; *Macfadyena unguis-cati* (L.) A. Gentry[1] (juv.) D-10001010 (int.) D-1000010, (ad.) D-1000010,R-0,P-0,L-4,T-170; *Oroxylum indicum* Vent.[3] D-1000010,S-0010010,R-1,P-0,L-12,T-260; *Parmentiera cerifera* Seem.[1] R-1,P-0,L-8,T-180; *Radermachera elmerei* Merr.[6] D-1000000,R-1,P-0,L-12,T-290; *Spathodea campanulata* Beauv.[3] R-1,P-0,L-11,T-310; *Stereospermum suaveolens* DC.[3] S-1000000,R-0,P-1,L-9,T-230; *Tabebuia argentea* Britt.[3] D-1000010,R-0,P-0,L-12,T-400; *Tabebuia heterophylla* (DC.) Britt.[1] D-1000000,S-1110000,R-1,P-0,L-10,T-420; *Tecoma stans* HBK.[2] R-0,P-0,L-10,T-110.

BIXACEAE *Bixa orellana* L.[1] R-1,P-1,L-19,T-140.

BLECHNACEAE *Blechnum brasiliensis* Desv.[3] D-0011000,R-0,P-0,L-35,T-160; *Blechnum serrulatum* ch.[3] D-0011000,R-0,P-0,L-15,T-24; *Stenochlaena tenuifolia* (Desv.) Moore[1] R-0,P-0,L-90,T-150.

BORAGINACEAE *Bourreria ovata* Miers[2] R-1,P-0,L-4,T-230; *Cordia alliodora* (Ruiz & Pavon) Oken[1] R-1,P-0,L-18,T-230; *Cordia boissieri* A. DC.[2] R-0,P-0,L-12,T-300; *Cordia lutea* Lam.[1] R-0,P-0,L-7,T-210; *Cordia sebestena* L.[3] R-1,P-0,L-10,T-310; *Tournefortia astrotricha* DC.[1] R-1,P-0,L-15,T-500.

BURSERACEAE *Boswellia sacra* Flueck. R-0,P-0,L-2,T-270; *Bursera inaguensis* Britt.[1] R-0,P-0,L-4,T-240; *Bursera simaruba* Sarg.[3] D-0011000,R-0,P-1,L-6,T-250; *Protium serratum* (Wall & Colebr.) Engl.[3] D-0010000,R-0,P-1,L-13,T-170.

CACTACEAE *Pereskia bleo* (HBK.) DC.[1] D-1000000,R-1,P-1; *Pereskia corrugata* Cutak[1] D-1011000,R-1,P-1.

CAPPARIDACEAE *Capparis cynophallophora* L.[4] R-1,P-0,L-4,T-370; *Crataeva nurvala* Buch.-Ham.[1] R-1,P-1,L-10,T-200.

CARICACEAE *Carica papaya* L.[1] R-0,P-1,L-29,T-180.

CECROPIACEAE *Cecropia palmata* Willd.[1] R-0,P-0,L-26,T-190.

CELASTRACEAE *Crossopetalum rhacoma* Crantz[2] R-1,P-0,L-3,T-310; *Jacquinia keyensis* Mez.[2] R-0,P-0,L-5,T-550; *Maytenus phyllanthoides* Benth.[2] D-0010000,R-1,P-0,L-5,T-440; *Schaeffera frutescens* Jacq.[2] R-1,P-0,L-4,T-330.

CHRYSOBALANACEAE *Chrysobalanus icaco* L.[3] D-1100000,R-1,P-0,L-5,T-350; *Licania michauxii* Prance[9] D-1000010,R-0,P-1,L-8,T-290; *Licania rigida* Benth.[2] D-1000010,R-0,P-0,L-12,T-290; *Licania tomentosa* (Benth.) Fritsch.[1] R-0,P-0,L-12,T-170.

CLUSIACEAE *Calophyllum inophyllum* L.[2] D-0010000,R-0,P-0,L-10,T-300; *Clusia rosea* Jacq.[2] R-1,P-0,L-16,T-850; *Garcinia spicata* Hook f.[1] D-0010000,R-0,P-0,L-8,T-460; *Mesua ferea* L.[1] D-0000100,R-0,P-0,L-7,T-180; *Rheedia macrophylla* Planch. & Triana[2] R-0,P-0,L-17,T-260.

COCHLOSPERMACEAE *Cochlospermum vitifolium* Willd. *ex* Spreng.[1] D-1000000,R-0,P-1,L-10,T-180.

COMBRETACEAE *Bucida buceras* L.[3] D-0010000,S-0010000,R-0,P-0,L-6,T-260; *Bucida spinosa* Jennings[1] D-0010000,S-0010000,R-1,P-0,L-1,T-350; *Combretum aubletii* DC.[1] D-0010000,R-1,P-0,L-9,T-180; *Conocarpus erectum* L.[1] S-0010000,R-0,P-1,L-9,T-370; *Laguncularia racemosa* Gaertn. f.[1] R-0,P-1,L-6,T-550; *Quisqualis indica* L.[1] D-0011000,S-0010000,R-1,P-0,L-11,T-190; *Terminalia arjuna* Wight & Arn.[4] D-0011000,S-0010000,R-0,P-1,L-14,T-360; *Terminalia catappa* L.[4] D-1000010,S-0010000,R-0,P-0,L-13,T-200; *Terminalia muelleri* Benth.[1] D-1000010,R-0,P-0,L-13,T-200.

CONVOLVULACEAE *Argyreia nervosa* Bojer[1] R-1,P-0,L-17,T-300; *Ipomoea carnea* Forst. f.[2] R-1,P-0,L-18,T-130; *Ipomoea pauciflora* Mart. & Gal.[1] R-0,P-0,L-13,T-190; *Ipomoea pes-caprae* Roth[1] R-1,P-1,L-6,T-510.

CYCADACEAE *Cycas circinalis* L.[6] R-0,P-0,L-28,T-380.

DILLENIACEAE *Dillenia indica* L.[6] S-0011000,R-0,P-0,L-31,T-240.

DIOSCOREACEAE *Dioscorea bulbifera* L.[2] D-0001000,R-0,P-1,L-10,T-150.

DRYOPTERIDACEAE *Nephrolepis exaltata* Davenport[2] R-0,P-1,L-11,T-180.

EBENACEAE *Diospyros digyna* Jacq.[2] R-0,P-0,L-18,T-270; *Diospyros virginiana* L.[2] R-0,P-1,L-13,T-240.

EUPHORBIACEAE *Acalypha hispida* Burm. F.[1] S-1010000,R-1,P-0,L-15,T-250; *Aleurites mollucana* Willd.[3] D-0000001,R-0,P-1,L-15,T-280; *Antidesma bunius* Spreng.[2] D-0011000,R-1,P-0,L-13,T-280; *Ateramnus lucidus* (Sw.) Rothm.[2] D-0011000,S-0010000,R-0,P-0,L-7,T-320; *Bischofia javanica* Blume[3] S-0011000,R-0,P-0,L-10,T-420; *Euphorbia leucocephala* Lotsy.[1] S-1010000,R-0,P-1,L-7,T-150; *Excoacaria bicolor* Hassk.[1] M-0000010; *Hippomane mancinella* L.[1] R-0,P-0,L-10,T-240; *Jatropha curcas* L.[1] D-1000010,R-1,P-0,L-15,T-230; *Jatropha gossypifolia* L.[1] D-0000010,R-1,P-0,L-10,T-280; *Macaranga gigantifolia* Merrill[1] D-0011000,R-1,P-1,L-49,T-230; *Phyllanthus acidus* Skeels[3] D-0001000,R-1,P-0,L-12,T-270; *Ricinus communis* L.[3] D-1000000,R-1,P-1,L-23,T-260; *Savia bahamense* Britt.[1] R-0,P-0,L-4,T-270.

FABACEAE-Caesalpinioideae *Bauhinia corymbosa* Roxb.[1] D-1000010,R-1,P-0,L-3,T-150; *Bauhinia purporea* L.[4] D-0000001,R-1,P-0,L-10,T-160; *Bauhinia roxburghiana* Voigt[1] D-1000010,R-0,P-0,L-8,T-230; *Brownea capitella* Jacq.[1] D-0001000,R-1,P-0,L-28,T-200; *Caesalpinia crista* L.[1] R-0,P-0,L-6,T-180; *Caesalpinia platyloba* S. Wats.[3] D-1000000,R-

1,P-1,L-6,T-220; *Caesalpinia pulcherrima* Swartz[1] D-1000000,R-1,P-0,L-2,T-120; *Caesalpinia vesicaria* Vell.[1] D-1000000,R-1,P-1,L-3,T-360; *Cassia alata* L.[3] R-0,P-1,L-14,T-180; *Cassia chapmanni* Isely[2] R-0,P-1,L-3,T-310; *Cassia fistula* L.[1] D-1000000,R-0,P-0,L-16,T-140; *Cassia ligustrina* L.[2] R-0,P-1,L-5,T-140; *Colvillea racemosa* Bojer[6] R-1,P-0,L-1,T-140; *Delonix regia* Raf.[4] R-1,P-0,L-1,T-200; *Peltophorum pterocarpum* Backer[3] R-1,P-0,L-1,T-140; *Pterocarpus marsupium* Roxb.[3] R-0,P-1,L-6,T-180; *Tamarindus indica* L.[3] D-1000010,R-1,P-0,L-2,T-140. -Mimosoideae *Acacia choriophylla* Benth. ex Hook.[3] R-0,P-1,L-2,T-170; *Acacia cornigera* (L.) Willd.[3] D-1000000,R-0,P-1,L-1,T-120; *Acacia farnesiana* (L.) Willd.[3] R-0,P-0,L-1,T-160; *Albizia lebbeck* Benth.[4] R-0,P-0,L-2,T-170; *Calliandra haematocephala* Hassk.[1] D-0011000,R-1,P-0,L-4,T-190; *Inga paterno* Harms[1] D-00100001,R-0,P-0,L-16,T-240; *Leucaena leucocephala* DeWit[7] R-0,P-0,L-1,T-140; *Lysiloma latisiliquum* Benth.[3] D-1000000,R-0,P-0,L-1,T-150; *Parkia javanica* (Lamk.) Merr.[3] R-0,P-0,L-1,T-90; *Pithecellobium guadalupense* (Pers.) Chapm.[2] R-1,P-0,L-6,T-210; *Pithecellobium unguis-cati* (L.) Benth.[2] D-1000010,R-1,P-0,L-4,T-130; *Prosopis juliflora* DC.[1] R-0,P-0,L-1,T-180. -Papilionoideae *Adenanthera pavonina* L.[3] D-1000010,R-1,P-1,L-4,T-180; *Butea monosperma* Kuntze[4] R-1,P-0,L-8,T-360; *Cajanus cajan* Millsp.[2] R-0,P-0,L-7,T-180; *Dalbergia brownei* Chapm.[8] R-0,P-0,L-7,T-230; *Dalbergia sissoo* Roxb.[3] R-0,P-0,L-7,T-230; *Erythrina herbacea* L.[4] R-1,P-0,L-4,T-220; *Erythrina variegata* Merr.[3] R-1,P-0,L-23,T-220; *Gliricidia sepium* (Jacq.) Walp.[2] R-1,P-0,L-5,T-220; *Lonchocarpus domingensis* (Pers.) DC.[1] D-0011000,R-1,P-0,L-9,T-230; *Piscidia piscipula* Sarg.[3] R-1,P-0,L-10,T-210; *Pongamia pinnata* Pierre[3] D-1001000,R-1,P-0,L-7,T-160; *Sophora tomentosa* L.[3] R-0,P-1,L-3,T-330; *Strongylodon macrobotrys* A.Gray[1] D-0010100,R-0,P-0,L-12,T-390.

FAGACEAE *Quercus virginiana* Mill.[3] D-0011000,R-1,P-1,L-4,T-370.

FLACOURTIACEAE *Casearia nitida* (L.) Jacq.[2] D-0011000,S-0010000,R-0,P-0,L-5,T-180; *Flacourtia indica* (Burm.f.) Merr.[2] D-0111000,S-0010000,R-1,P-0,L-7,T-230; *Oncoba spinosa* Forsk.[2] D-0001000,S-0010000,R-0,P-0,L-8,T-170; *Zuelania guidonii* (Sw.) Britt. & Millsp.[1] D-0011000,S-0010000,R-0,P-0,L-10,T-250.

GESNERIACEAE *Episcia lilacina* Hanst.[5] M-0001010.

GOODENIACEAE *Scaevola plumerei* (L.) Vahl[2] R-1,P-0,L-8,T-960.

GNETACEAE *Gnetum gnemon* L.[3] R-1,P-0,L-23,T-240.

HELICONIACEAE *Heliconia zebrina* Plowman, Kress & Kennedy[1] M-0000010.

HUMIRIACEAE *Drypetes diversifolia* Krug. & Urb.[2] R-1,P-0,L-8,T-300; *Drypetes laterifolia* (Sw.) Krug. & Urb.[2] R-1,P-0,L-9,T-240.

LAURACEAE *Cinnamomum verum* J. Presl.[3] D-0010010,R-0,P-0,L-13,T-200; *Licaria triandra* (Sw.) Kostermans[2] D-0001000,R-1,P-0,L-8,T-230; *Nectandra coriacea* (Sw.) Griseb.[3] R-1,P-0,L-9,T-210; *Persea americana* Mill.[3] D-0011000,R-0,P-0,L-19,T-250; *Persea borbonia* (L.) K. Spreng.[3] R-1,P-0,L-9,T-230.

LECYTHIDACEAE *Barringtonia racemosa* Roxb.[1] D-0001000,R-1,P-1,L-24,T-280; *Couroupita guianensis* Aubl.[1] D-0010100,R-1,P-1,L-28,T-160; *Gustavia poeppigiana* Berg.[1] D-0000100,R-1,P-0,L-50,T-220; *Gustavia superba* (HBK.) Berg.[1] D-0011000,R-1,P-0,L-57,T-210.

LOGANIACEAE *Buddleja madagascariensis* Lam.[2] R-0,P-0,L-16,T-220; *Fagraea ceilanica* Thunb.[1] R-0,P-0,L-21,T-330; *Strychnos spinosa* Lam.[2] R-0,P-0,L-7,T-290.

LYTHRACEAE *Duabanga sonneratioides* Buch-Ham.[1] D-0011000,R-0,P-1,L-23,T-310; *Ginoria glabra* Griseb.[1] D-0010000,D-0011000,R-1,P-0,L-7,T-230; *Lagerstromia indica* L.[1] D-0011000,S-0010000,R-1,P-1,L-8,T-220; *Lagerstromia speciosa* (L.) Pers.[1] D-0001000,S-0010000,R-1,P-1,L-19,T-300; *Lawsonia inermis* L.[1] D-0010000,R-1,P-1,L-3,T-270.

MAGNOLIACEAE *Magnolia grandiflora* L.[4] R-1,P-0,L-7,T-420; *Magnolia virginiana* L.[7] D-0100000,R-1,P-0,L-8,T-280; *Michelia champaca* L.[1] R-1,P-0,L-24,T-160.

MALPIGHIACEAE *Byrsonima crassifolium* (L.) HBK.[2] S-0011000,R-1,P-0,L-3,T-300; *Byrsonima lucida* (Mill.) DC.[2] D-0010000,R-1,P-0,L-4,T-300; *Galphimia gracilis* Bartl.[1] S-1000000,R-1,P-1,L-3,T-210; *Hiptage benghalensis* (L.) Kurz[1] D-0011000,R-1,P-0,L-19,T-250; *Malpighia coccigera* L.[1] D-0010000,S-0010000,R-1,P-0,L-4,T-280; *Stigmaphyllum sagraeanum* A. Juss.[1] D-0010000,R-0,P-1,L-7,T-280.

MALVACEAE *Adansonia digitata* L.[3] R-1,P-0,L-8,T-180; *Bombacopsis quinata* (Jacq.) Dug.[3] D-1000010,R-1,P-1,L-14,T-290; *Bombax ceiba* L.[3] D-0010100,R-1,P-0,L-12,T-180; *Carpodiptera ameliae* Cam. Lundell[1] D-0000001,S-0010000,R-0,P-0,L-24,T-220; *Ceiba pentandra* Gaertn.[3] D-0011000,R-1,P-0,L-17,T-210; *Chorisa speciosa* St. Hil.[3] D-0010100,R-1,P-0,L-13,T-170; *Dombeya perrieri* Arènes[2] D-0000101,S-0011000,R-1,P-1,L-11,T-190; *Dombeya wallichi* Daydon Jackson[1] R-1,P-0,L-16,T-240; *Gossypium hirsutum* L.[1] S-1000000,R-1,P-1,L-8,T-250; *Guazuma ulmifolia* Lam.[1] D-0000101,R-0,P-0,L-12,T-240; *Heliocarpus appendiculatus* Turcz.[1] R-0,P-1,L-17,T-140; *Heritieria littoralis* Dry.[1] D-1000000,R-1,P-0,L-20,T-320; *Hibiscus hastatus* L. f.[1] D-0001000,R-1,P-1,L-12,T-280; *Hibiscus rosa-sinensis* L.[4] R-1,P-1,L-8,T-290; *Hibiscus tiliaceus* L.[3] D-0001000,R-1,P-0,L-11,T-310; *Pachira aquatica* Aubl.[3] R-1,P-0,L-22,T-340; *Pavonia bahamensis* Hitchcock[1] R-0,P-0,L-6,T-450; *Pseudobombax ellipticum* Dugand[1] D-0011000,R-1,P-0,L-21,T-250; *Pterospermum acerifolium* (L.) Willd.[2] R-0,P-0,L-25,T-330; *Sterculia ceramica* R. Br.[1] R-1,P-0,L-17,T-180; *Sterculia foetida* L.[1] D-0010100,R-1,P-0,L-18,T-270; *Sterculia macrophylla* Vent.[3] D-0000001,R-1,P-0,L-30,T-360; *Theobroma cacao* L.[1] D-0000101,R-1,P-0,L-35,T-190; *Thespesia grandiflora* DC.[1] D-0001000,R-1,P-1,L-22,T-230; *Thespesia populnea* Soland.[4] R-1,P-0,L-12,T-280.

MARANTACEAE *Calathea micans* (Mathieu) Koern.[6] M-0000010; *Calathea roseapicta* (Lind.) Reg.[1] M-0000010.

MARATTIACEAE *Angiopteris evecta* (Forster f.) Hoffm.[3] R-0,P-0,L-18,T-340.

MARCGRAVIACEAE *Marcgravia rectiflora* Triana & Planch.[1] (juv.) D-0011000,L-2,T-300 (ad.) D-0011000,R-1,P-0,L-12,T-430.

MELASTOMATACEAE *Leandra dichotoma* (D.Don) Cogn.[6] M0000011; *Medinella myriantha* Merr.[1] D-0001000,R-1,P-0,L-16,T-450; *Monolaena primulaeflora* Hook. f.[1] M-0001010; *Tetrazygia bicolor* (Miller) Cogn.[3] D-1000000,S-1110000,R-1,P-0,L-9,T-300; *Tibouchina urvil-*

leana Cogn.[3] S-0010000,R-1,P-0,L-8,T-450; *Triolena hirsuta* (Benth.) Triana[6] M-0001000.

MELIACEAE *Azadirachta indica* A. Juss.[3] D-1000000,R-0,P-0,L-6,T-200; *Carapa guianensis* Aublet[3] D-1001000,R-0,P-0,L-21,T-170; *Cedrela odorata* L.[1] R-0,P-0,L-12,T-150; *Cedrela toona* Roxb.[1] D-1000000,R-0,P-0,L-11,T-160; *Chukrasia tabularis* A. Juss.[1] D-1000010,R-1,P-0,L-16,T-230; *Guarea glabra* Vahl[3] D-0001000,R-1,P-0,L-14,T-230; *Melia azadirach* L.[4] R-1,P-1,L-6,T-150; *Sandoricum koetjape* (Burm. f.) Merr.[6] D-0011000,S-0011000,R-0,P-0,L-24,T-240; *Swietenia macrophylla* King[3] D-0000010,R-0,P-0,L-22,T-250; *Swietenia mahagoni* Jacq.[3] D-1000000,R-0,P-1,L-6,T-230; *Trichilia hirta* L.[1] R-0,P-0,L-9,T-140.

MENISPERMACEAE *Cocculus laurifolius* DC.[2] R-0,P-0,L-14,T-180.

MENYANTHACEAE *Nymphoides aquatica* (J. F. Gmel.) Knutze[7] M-0000010.

MORACEAE *Artocarpus heterophyllus* Lam.[6] R-0,P-0,L-12,T-340; *Ficus altissima* Blume[4] R-1,P-0,L-21,T-310; *Ficus aurea* Nutt.[1] R-1,P-0,15,T-380; *Ficus benghalensis* L.[1] D-0011000,R-1,P-0,L-20,T-300; *Ficus benjamina* L.[4] R-1,P-0,L-8,T-240; *Ficus carica* L.[3] R-0,P-0,L-12,T-280; *Ficus citrifolia* Mill.[2] D-0010000,R-1,P-0,L-10,T-280; *Ficus elastica* Roxb.[4] D-0011000,R-0,P-0,L-27,T-760; *Ficus pumila* L.[3] (juv.) D-0001010 (ad.) D-0001000,R-0,P-1,L-5,T-290; *Ficus religiosa* L.[4] D-0011000,R-1,P-0,L-20,T-230; *Morus rubra* L.[3] R-1,P-0,L-23,T-170.

MORINGACEAE *Moringa oleifera* Lam.[3] R-0,P-1,L-1,T-180.

MUNTINGIACEAE *Muntingia calabura* L.[2] R-1,P-0,L-14,T-170.

MYRICACEAE *Myrica cerifera* L.[3] R-0,P-0,L-6,T-290.

MYRSINACEAE *Ardisia escallonioides* Sch. & Cham.[2] R-1,P-1,L-9,T-270; *Ardisia solanacea* Roxb.[3] D-0011000,R-1,P-1,L-11,T-320; *Myrsine floridana* A. DC.[3] R-1,P-0;,L-7,T-280; *Wallenia laurifolia* Sw.[1] D-1000010,R-1,P-0,L-8,T-300.

MYRTACEAE *Callistemon viminalis* Cheel.[3] D-0011000,R-1,P-1,L-6,T-300; *Calyptranthes zuzygium* (L.) Sw.[2] D-0010000,R-1,P-0,L-7,T-300; *Eucalyptus deglupta* Sm.[1] D-0111010,S-0010000,R-0,P-0,L-15,T-190; *Eucalyptus torelliana* F. Muell.[3] D-1000011,R-0,P-1,L-11,T-280; *Eugenia axillaris* (Sw.) Willd.[2] D-0010000,R-1,P-1,L-5,T-350; *Eugenia foetida* Pers.[2] D-0010000,R-1,P-1,L-4,T-330; *Eugenia rhombea* (Berg) Krug. & Urb.[1] D-0010000,R-1,P-0,L-4,T-400; *Eugenia uniflora* L.[4] D-0010000,R-1,P-0,L-3,T-210; *Melaleuca quinquenervia* S. T. Blake[1] D-0010000,R-0,P-1,L-7,T-330; *Myrcianthes fragrans* (Sw.) McVaugh[1] D-0110000,R-1,P-0,L-4,T-320; *Pimenta dioica* (L.) Merr.[3] R-0,P-0,L-12,T-280; *Psidium guajava* L.[6] D-0010000,S-1110000,R-1,P-0,L-9,T-320; *Syzygium cumini* Skeels[3] D-1011000,R-1,P-0,L-19,T-420; *Syzygium jambos* Alston[3] D-0010000,R-1,P-0,L-19,T-240.

NYCTAGINACEAE *Boerhavia diffusa* L.[6] R-1,P-0; *Bougainvillea spectabilis* Willd.[1] D-1000000,R-1,P-1; *Guapira longifolia* (Heimerl) Little[2] R-1,P-0; *Guapira discolor* (K. Spreng.) Little[2] R-1,P-0; *Mirabilis jalapa* L.[4] R-1,P-0; *Neea psychotrioides* J.D. Sm.[5] D-1000010,R-1,P-1; *Pisonia aculeata* L.[2] D-0010000,R-0,P-1; *Pisonia rotundata* Griseb.[2] R-0,P-0.

NYMPHAEACEAE *Nuphar luteum* (L.) Sibth. & Sm.[7] D-1000010,R-0,P-0,L-17,T-530; *Nymphaea odorata* Ait.[7] M-0000010.

OCHNACEAE *Ochna mossambicensis* Klotzsch[1] D-0011000,R-1,P-0,L-12,T-210.

OLEACEAE *Forestiera pinetorum* Small[2] R-0,P-0,L-4,T-240; *Fraxinus caroliniana* Miller[2] S-1100000,R-0,P-0,L-6,T-170; *Jasminum fluminense* Vell.[4] R-1,P-0,L-4,T-160; *Jasminum multiflorum* Andr.[4] R-1,P-0,L-4,T-160; *Ligustrum japonicum* Thunb.[3] R-1,P-0,L-7,T-530; *Noronhia emarginata* (Lam.) Poir.[2] R-0,P-0,L-13,T-480; *Nyctanthes arbor-tristis* L.[4] R-0,P-0,L-10,T-330. ONAGRACEAE *Ludwigia repens* Forst.[7] M-0001010.

ORCHIDACEAE *Ludisia discolor* A. Rich.[3] M-0001000; *Sobralia madisonii* Dodson[3] M-1000010.

OXALIDACEAE *Averrhoa carambola* L.[2] D-1000010,R-1,P-1,L-7,T-210; *Averrhoa bilimbi* L.[2] D-1000010,R-1,P-0,L-6,T-130.

PHYTOLLACACEAE *Petivaria alliacea* L.[8] R-1,P-0; *Phytollaca dodecandra* Kunth & Bouché[1] R-1,P-0; *Phytollaca rivinoides* Kunth & Bouché[5] R-1,P-1; *Rivina humilis* L.[8] R-1,P-1.

PIPERACEAE *Piper amalago* L.[1] R-0,P-0,L-10,T-220; *Piper auritum* HBK.[1] R-0,P-1,L-26,T-210; Piper crocatum Ruiz & Pavon[3] M-0001000.

PITTOSPORACEAE *Pittosporum pentandrum* (Blanco) Merrill[2] R-0,P-0,L-18,T-150; *Pittosporum tobira* Ait. R-1,P-0,L-5,T-320.

PODOCARPACEAE *Podocarpus gracilior* Pilg.[4] R-0,P-0,L-4,T-390.

POLYGONACEAE *Coccoloba diversifolia* Jacq.[3] D-0000100,R-1,P-0,L-7,T-250; *Coccoloba uvifera* Jacq.[3] D-0000100,S-1110000,R-1,P-1,L-16,T-440; *Ruprechtia coriacea* Benth. & Hook. f.[1] D-0000010,R-1,P-0,L-16,T-270; *Triplaris cumingiana* Fisch. & Mey.[6] D-0011000,R-1,P-0,L-28,T-150.

POLYPODIACEAE *Drynaria quercifolia* (L.) J. Sm.[3] R-0,P-0,L-45,T-190; *Polypodium polypodioides* var. *michauxianum* Weath.[3] R-0,P-0,L-8,T-310.

PORTULACACEAE *Portulaca amilis* Speg.[3] R-1,P-1; *Portulacaria afra* Jacq.[1] R-1,P-1.

PROTEACEAE *Grevillea robusta* Cunn.[1] R-1,P-0,L-8,T-250; *Macadamia integrifolia* Maiden & Betche[3] R-0,P-0,L-15,T-280; *Oreocallis wickhamii* F. Muell.[1] R-1,P-0,L-35,T-290.

PTERIDACEAE *Acrostichum aureum* L.[1] R-0,P-0,L-21,T-240; *Adiantum cappilis-veneris* L.[1] D-1000000,R-0,P-0,L-1,T-110.

RHAMNACEAE *Colubrina cubense* (Jacq.) Brongn.[2] R-0,P-0,L-16,T-200; *Colubrina elliptica* (Sw.) Briz. & Stern[2] R-1,P-1,L-8,T-180; *Krugiodendron ferreum* (Vahl) Urb.[2] D-0010000,R-0,P-0,L-5,T-190; *Reynosia septentrionalis* Urb.[2] D-0100100,R-1,P-1,L-3,T-370; *Zizyphus mauritiana* Lam.[1] R-0,P-0,L-5,T-300.

RHIZOPHORACEAE *Rhizophora mangle* L.[1] D-0001000,R-0,P-0,L-8,T-490.

ROSACEAE *Eryobotrea japonica* (Thunb.) Lindley[3] R-0,P-0,L-18,T-320; *Prunus myrtifolia* (L.) Urban[2] R-1,P-0,L-8,T-220; *Raphiolepis umbellata* Makino[1] D-0010000,S-0010000,R-1,P-1,L-5,T-510; *Rosa multiflora* Thunb.[4] D-1000010,R-1,P-1,L-6,T-170.

RUBIACEAE *Adina cordifolia* Benth & Hook. f.[1] R-0,P-

1,L-14,T-240; *Antirhea lucida* (Sw.) Benth. & Hook. f.[2] D-0011000,S-0011000,R-1,P-0,L-6,T-210; *Casasia clusiaefolia* Urban[2] R-1,P-0,L-16,T-460; *Cephalanthus occidentalis* L.[7] D-0011000,S-0011000,R-0,P-1,L-12,T-230; *Chiococca alba* Hitch.[2] R-0,P-0,L-6,T-290; *Coffea arabica* L.[1] D-0010000,R-1,P-0,L-12,T-230; *Erithalis fruticosa* L.[2] R-1,P-0,L-6,T-450; *Exostema caribaea* (Jacq.) Roemer & Schultes[2] S-1010000,R-0,P-0,L-5,T-200; *Gardenia jasminoides* Ellis[4] R-0,P-0,L-4,T-280; *Guettarda ellipta* Sw.[2] R-1,P-0,L-3,T-250; *Guettarda scabra* (L.) Vent.[2] S-0011000,R-1,P-0,L-8,T-470; *Guettarda speciosa* L.[1] R-1,P-0,L-22,T-240; *Hamelia cuprea* Griseb.[1] S-0011000,R-1,P-1,L-6,T-250; *Hamelia patens* Jacq.[3] D-0011000,S-0010000,R-1,P-1,L-7,T-200; *Hoffmania ghiesbrechtii* Hemsl.[1] M-0001000; *Ixora coccinea* L.[3] D-0011000,R-1,P-1,L-13,T-320; *Ixora duffyi* T. Moore[2] D-0101000,R-1,P-0,L-14,T-310; *Morinda citrifolia* L.[2] R-0,P-1,L-8,T-240; *Mussaenda erythrophylla* Schum. & Thonn.[1] R-1,P-0,L-9,T-230; *Pentas lanceolata* Deflers[3] R-1,P-0,L-4,T-350; *Portlandia grandifolia* L.[1] D-0010000,R-1,P-0,L-15,T-520; *Psychotria microbotrys* Ruiz ex standley[5] M-0000010; *Psychotria nervosa* Sw.[2] R-1,P-0,L-10,T-170; *Psychotria sulznerii* Small[1] R-1,P-0,L-12,T-200; *Randia aculeata* L.[2] R-1,P-0,L-2,T-260.

RUTACEAE *Aegle marmelos* Correa *ex* Roxb.[4] D-1000010,R-0,P-1,L-7,T-320; *Amyris elemifolia* L.[2] D-1000000,R-1,P-0,L-5,T-290; *Casimaroa edulis* Llave & Lex.[1] D-1000000,R-0,P-0,L-22,T-200; *Citrus aurantifolia* Swingle[4] R-0,P-0,L-10,T-200; *Citrus paradisii* Macf.[4] R-0,P-0,L-8,T-240; *Fortunella margarita* (Lour.) Swingle[3] R-2,P-0,L-8,T-330; *Murraya koenigii* (L.) Swingle[4] D-1000000,R-0,P-1,L-5,T-160; *Murraya paniculata* Jack[1] R-1,P-0,L-3,T-240; *Triphasia trifolia* P. Wils.[1] R-1,P-1,L-4,T-310; *Zanthoxylon fagara* Sang.[2] R-0,P-0,L-3,T-260.

SALICACEAE *Salix caroliniana* Michx.[7] D-0011000,R-0,P-0,L-11,T-170.

SAPINDACEAE *Acer rubrum* L.[3] D-0010000,S-0011000,R-1,P-1,L-9,T-180; *Blighia sapida* Kon.[2] D-0010100,R-1,P-0,L-17,T-200; *Dimocarpus longan* Lour.[2] D-0011000,R-1,P-0,L-14,T-250; *Dodonaea viscosa* (L.) Jacq.[2] R-1,P-0,L-9,T-190; *Exothea paniculata* (Juss.) Radlk.[2] R-1,P-0,L-8,T-130; *Filicium decipiens* (Wight & Arn.) Hook. f.[4] R-1,P-0,L-10,T-200; *Harpullia arborea* Radlk.[6] R-1,P-0,L-18,T-170; *Hypalete trifoliata* Sw.[1] R-1,P-0,L-4,T-340; *Kolreuteria elegans* A. C. Smith[3] D-0000010,R-1,P-1,L-7,T-150; *Litchi chinensis* Sonn.[4] D-0010000,R-1,P-0,L-12,T-230; *Nephelium malaiense* Griff.[3] D-1010000,R-0,P-0,L-23,T-150; *Sapindus saponaria* L.[3] R-0,P-0,L-9,T-160.

SAPOTACEAE *Bumelia celastrina* HBK.[2] R-1,P-0,L-3,T-480; *Chrysophyllum oliviforme* L.[4] S-0010000,R-1,P-0,L-9,T-360; *Dipholis salicifolia* (L.) DC.[3] R-1,P-0,L-11,T-210; *Manilkara bahamensis* Lam. & Meeuse[3] R-0,P-0,L-8,T-370;

Manilkara zapota Royen.[3] D-0110100,R-0,P-0,L-9,T-240; *Mastichodendron foetidissimum* H.J. Lam.[2] R-0,P-0,L-16,T-150; *Mimusops elengi* L.[2] R-0,P-0,L-12,T-230; *Mimusops roxburgiana* Wight[3] R-0,P-0,L-13,T-490; *Pouteria campechiana* Baehni[9] S-0010000,R-0,P-0,L-11,T-150; *Pouteria sapota* H. E. Moore & Stearn[1] R-0,P-0,L-25,T-220.

SIMAROUBACEAE *Alvaradoa amorphioides* Liebm.[2] R-0,P-1,L-2,T-160; *Picramnia pentandra* Sw.[3] D-0011000,S-1010000,R-1,P-1,L-9,T-190; *Simarouba glauca* DC.[3] D-1000000,S-1000000,R-1,P-0,L-8,T-330.

SMILACACEAE *Smilax laurifolia* L.[2] D-0011000,R-0,P-0,L-8,T-220.

SOLANACEAE *Brugmansia aurea* Lagerh.[1] R-1,P-0,L-18,T-230; *Brugmansia suaveolens* Bercht. & Presl[4] R-1,P-0,L-20,T-250; *Brunsfelsia uniflora* G. Don[1] R-1,P-0,L-7,T-380; *Cestrum nocturnum* L.[3] R-1,P-0,L-7,T-280; *Solandra nitida* Zucc.[1] R-1,P-0,L-12,T-310.

TURNERACEAE *Turnera ulmifolia* L.[3] R-0,P-0,L-6,T-220.

ULMACEAE *Celtis laevigata* Willd.[2] R-1,P-0,L-7,T-160; *Holoptelia integrifolia* Planch.[3] D-1010010,R-0,P-0,L-8,T-200; *Trema micranthum* (L.) Blume[3] R-0,P-0,L-6,T-380.

VERBENACEAE *Avicennia germinans* Stearn[1] R-0,P-0,L-8,T-480; *Callicarpa americana* L.[2] R-1,P-0,L-9,T-300; *Citharexylum fruticosum* L.[2] R-1,P-1,L-9,T-290; *Clerodendron paniculatum* L.[4] R-1,P-1,L-20,T-230; *Clerodendron quadriloculare* (Blanco) Merr.[1] M-0000010; *Clerodendron splendens* G. Don[1] R-1,P-1,L-11,T-220; *Congea tomentosa* Roxb.[1] R-1,P-1,L-14,T-210; *Duranta repens* L.[4] R-1,P-0,L-4,T-170; *Gmelina arborea* Roxb.[1] R-1,P-1,L-16,T-140; *Holmskoldia sanguinea* Retz[1] R-1,P-0,L-9,T-220; *Lantana camara* L.[3] R-1,P-0,L-7,T-180; *Petrea volubilis* Jacq.[1] R-1,P-0,L-12,T-230; *Stachytarpheta jamaicensis* (L.) Vahl.[4] R-1,P-0,L-4,T-230; *Tectona grandis* L. f.[6] D-0010000,R-0,P-0,L-38,T-200; *Vitex agnus-castus* L.[2] D-0001000,S-1000000,R-1,P-1,L-9,T-180; *Vitex trifolia* L.[2] R-1,P-0,L-6,T-200.

VITACEAE *Cissus discolor* Bl.[3] M-0000010; *Leea guineensis* G. Don[1] D-0011000,R-1,P-1,L-11,T-190; *Parthenocissus quinquefolia* (L.) Planch.[3] D-1000010,S-0010000,R-1,P-1,L-6,T-210; *Vitis rotundifolia* Michx.[3] D-1000010,R-1,P-1,L-6,T-200.

ZAMIACEAE *Ceratozamia robusta* Miq.[1] R-0,P-0,L-42,T-510; *Zamia fischeri* Miq.[1] R-1,P-0,L-8,T-210; *Zamia integrifolia* Ait.[1] R-1,P-0,L-10,T-430.

ZINGIBERACEAE *Costus scaber* Ruiz & Pavón[5] M-0000010; *Globba atrosanguinea* Teysm. & Binn.[1] M-0000010; *Kaempfera pulchra* Ridl.[1] M-0001000.

ZYGOPHYLLACEAE *Bulnesia arborea* (Jacq.) Engl.[3] R-0,P-0,L-3,T-210; *Guaiacum officinale* L.[1] D-1000010,R-1,P-1,L-4,T-200; *Guaiacum sanctum* L.[1] R-1,P-0,L-3,T-200; *Tribulus cistoides* L.[4] R-0,P-0,L-1,T-230.

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