LEAF FLUSHING AS TAXONOMIC EVIDENCE OF SOME DIOSPYROS SPECIES

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Eva Kristinawati Putri & Tatik Chikmawati. 2015. Pemoposan Sebagai Bukti Taksonomi Beberapa Jenis *Diospyros*. *Floribunda* 5(2): 31–47. — Kita cenderung menggunakan struktur generatif untuk identifikasi tanaman, meskipun ketersediaan struktur generatif di lapangan seringkali menjadi masalah bagi praktik identifikasi tanaman yang berbuah hanya sekali dalam setahun, seperti pada *Diospyros* L. (*Ebenaceae*). Pemoposan (*leaf flushing*) masih jarang digunakan dan implikasi taksonominya belum pernah diperhitungkan. Penelitian ini mempelajari pemoposan dan implikasi taksonominya pada delapan jenis *Diospyros* di Ecopark Cibinong Science Center LIPI, Bogor (Jawa Barat). Observasi karakter morfologi dilakukan pada tiga cabang (masing-masing memiliki tiga set pemoposan dan sebuah kuncup apikal dorman) pada 22 individu *Diospyros*. Perkembangan kuncup *Diospyros* menghasilkan satu set pemoposan yang dapat dibedakan dengan set pemoposan yang sebelumnya. Pemoposan setelah periode dormansi dan adanya daun tereduksi pada beberapa spesies mengindikasikan adanya ritme pertumbuhan kuncup. Pemoposan dapat ditemukan beberapa bulan sekali atau di sepanjang tahun dengan membutuhkan waktu 40–55 hari hingga terbentuknya daun dewasa. Pemoposan menyediakan 39 karakter yang dapat digunakan sebagai bukti taksonomi untuk membedakan delapan jenis *Diospyros* berikut dengan kunci identifikasinya.

Kata kunci: *Diospyros*, pemoposan, bukti taksonomi

Eva Kristinawati Putri & Tatik Chikmawati. 2015. Leaf Flushings as Taxonomic Evidence of Some *Diospyros* Species. *Floribunda* 5(2): 31–47. — People tend to use generative structures for plant identification. Nevertheless, generative structure availibility limits the identification practice for a plant with once-a-year fruit-bearing phase, such as *Diospyros* L. (*Ebenaceae*). Being vegetative characters, leaf flushing are rarely used for plant identification so that they have not been explored as a taxonomic evidence. In this paper, leaf flushings and their taxonomic implication were studied using eight species of *Diospyros* grown in Ecopark of Cibinong Science Center LIPI, Bogor (West Java). Observations on morphological characters were undertaken on three twigs (which have three flushing sets and an apical dormant bud) taken from each 22 individual trees of *Diospyros* species available. Morphological development observation showed that bud rhythmic growth produce flushing sets usually distinguishable from the previous sets. Leaf flushing time after a period of dormancy and the presence of small reduced leaf in some species indicated an arrested growth in the bud. Leaf flushings can be found every few months or all year around with a period of 40–55 days for the formation of mature leaves. Leaf flushing provided 39 characters that can be used as taxonomic evidence for distinguishing the eight species of *Diospyros* observed. A determination key for these species solely based on leaf flushing characters is presented.

Keywords: *Diospyros*, leaf flushing, taxonomic evidence

Most species of *Diospyros* are black barked, evergreen and dioecious trees with trunk bearing spirally arranged leaves (Wallnöfer 2001; Ng 2002). There are 500–600 *Diospyros* species worldwide, mostly distributed in tropical regions (Bakhuizen van den Brink 1936; Ng 2002; Kerrigan *et al*. 2011). Some *Diospyros* have a high commercial value for their timber and fruit. “Black ebony ” (*D. ferrea* and *D. ebenum*) and “streaked ebony” (*D. blancoi, D. celebica*, and *D. pilosanthera*) are famous timber product for their black heartwood with red-brown pattern (Walujo 2000). The most famous *Diospyros* edible fruit is *D. kaki* (Ng 2002).

Diospyros identification has been done using the combination of characters of mature leaf, flower, and fruit (Ridley 1923; Bakhuizen van den Brink 1936; Backer & Bakhuizen van den Brink 1965; Corner 1988). Generally, *Diospyros* produces generative structures once a year. This can become the delimitation for their identification practice. Therefore, a different alternative character for *Diospyros* identification is needed.

Personal observation of *Diospyros* showed some unique leaf flushing characters including red young leaves and the presence of small reduced leaf among other normal leaves that were much larger in size. The presence of this small leaf was seen by Wallnöfer (2001). However, the explanation he gave is merely information that reduced leaves, sometimes even appearing like a scale, are common to *Diospyros*. Perusals to literatures revealed that its taxonomic implication has not been studied yet.

Leaf flushing characters that have been used for plant identification in general were the colour of young leaf and ptyxis (way in which an individual expanded young leaf is folded). The red colour of young leaves was mentioned as a potential character but it cannot be widely used because it is not always available in the herbarium notes (Balgooy 1977). Observations on 187 families, 1000 genera and approximately 2000 species of plants indicated that ptyxis has the potential to be a taxonomic evidence (Cullen 1978). It was stated that three species of *Diospyros* have ptyxis variation, i.e. supervolute for *D. wilsonii,* conduplicate for *D. ferea* and *D. hawaiinensis*. Therefore, ptyxis has the potential to be used for *Diospyros* identification.

The objectives of the present study were to describe 1) leaf flushing morphological developments of *Diospyros*, 2) leaf flushing phenology of *Diospyros*, 3) leaf flushing morphological variations of *Diospyros*, 4) taxonomic implication of *Diospyros* leaf flushing characters, and 5) phenetic relationships among *Diospyros* species based on leaf flushing characters.

METHODOLOGY

Research Time and Place

This study was conducted from March 2012 to March 2013. Observation were confined to *Diospyros* species cultivated in Ecology Park Cibinong Science Centre LIPI, Bogor (West Java). It is an *ex-situ* conservation site of lowland ecosystem flora in Indonesia. It consists of a 32 hectares area which is divided into seven ecoregions according to the names of the Indonesian main islands (Sumatera, Jawa-Bali, Kalimantan, Sulawesi, Maluku, Nusa Tenggara and Papua). The observations were done at the same place to minimize the environmental factor involved so that the characters observed were genetically regulated. Besides Ecopark CSC-LIPI, the field observations were conducted in Bogor Botanical Garden, the courtyard of Herbarium Bogoriense Juanda Bogor and Faculty of Animal Science at Dramaga campus of Bogor Agricultural University.

Observation Techniques

Eight *Diospyros* species were observed, i.e. *D. malabarica* (Desr.) Kostel, *D. beccarioides* Ng, *D. buxifolia* (Blume) Hiern, *D. jaherii* Bakh., *D. blancoi* A. DC., *D. celebica* Bakh., *D. cauliflora* Blume and *D. pilosanthera* Blanco. Each species was represented by at least 2–5 individual trees. Three qualified twigs from each individual tree were marked at the first day of observation. Each twig consisted of three previous leaf flushing sets and an apical dormant bud. Two previous flushing sets were morphologically characterized as the mature flushing set. The early flushing set characters, including leaf flushing morphological development stages and some other morphological characters, were observed when the dormant bud was breaking-up. The observations were done twice a week, from the bud phase to the phase where the mature leaf has formed from its bud. The mature flushing set was morphologically characterized as the third flushing set from the twig.

Morphological Development Observation

The terminology used in morphological development observations is based on the list of Lawrence (1955), Hickey (1979), and Radford (1986). Ptyxis and vernation (the way in which leaves parts are folded or arranged in the bud in relation to one another) were first observed by Cullen (1978) and Bell (1991). Indumentum closure and vernation were observed by a hand-lens with 20 times magnification. These observations provided leaf flushing morphological development data and morphological characters. Leaf flushing morphological characters included bud, young leaf, mature leaf and flushing set (Table 1). *Diospyros blancoi* was used as a morphological development model for the *Diospyros* observed because of their large size of cataphylls (1–2 cm), short flushing set (4–9 foliage leaves) and long availibility of flushing leaves.

Phenological Observation

Leaf flushing phenological observations were done by documenting the time of bud break and the periode required to complete each leaf flushing stage. Leaf flushing stages included the expanding of all young leaves from the bud and the formation of mature flushing set. Leaves of mature flushing set have a maximal size and similar green colour with the previous flushing set. In every ob-

Table 1. Morphological characters for the phenetic analysis

No	Characters	Character set (code)
1.	the colour of early bud	Green (0), brown (1)
2.	indumentum closure of the early bud	Glabrous (0), pubescent (1), sericeous (2)
3.	indumentum colour of the early bud	None (0), silver-brown (1), white (2)
4.	the length of dormant bud	≤ 0,5 cm (0), 0,6–0,9 cm (1), ≥ 1 cm (2)
5.	the colour of dormant bud	Black (0), brown (1)
6.	indumentum closure of dormant bud	Glabrous (0), pubescent (1), sericeous (2)
7.	indumentum colour of dormant bud	None (0), black (1), silver-brown (2)
8.	flushing set	Indistingushable (0), distinguishable (1)
9.	the presents of cataphyll	Absent (0), present (1)
10.	the number of cataphyll	Absent (0), always one (1), more than one (2)
11.	the presents of dorsal cataphyll	Absent (0), present (1)
12.	petioles length in a flushing set	Uniform (0), patterned (1)
13.	the colour of young leaves	Red (0), pale green (1)
14.	ptyxis	Involute (0), conduplicate (1), plane (2), revolute (3)
15.	internodus length in a flushing set	Uniform (0), patterned (1)
16.	leaf size in a flushing set	Not observed (0), enlarge from the base to the middle set and become smaller to the set apex (1), uniform, sometimes smaller in the set base and apex (2), enlarged from the base to the middle set and same big to the set apex or sometimes smaller only on its set apex (3), enlarged to the set apex or smaller only on its set apex (4)
17.	indumentum closure of petioles	Glabrous (0), glabrescent (1), puberulous (2), glabrescent-glabrous, glabrescent on the base and glabrous on the apex of set (3)
18.	leaf shape in a flushing set	Not observed (0), varied (1), patterned (2), uniform (3)
19.	leaf shape at the set base	Not observed (0), lanceolate/narrowly elliptic (1), narrowly elliptic (2), elliptic (3), elliptic/circular (4), oblanceolate-narrowly elliptic (5)
20.	leaf shape at the middle set	Not observed (0), narrowly elliptic-narrowly oblong (1), narrowly elliptic (2), elliptic (3), elliptic-narrowly elliptic (4), narrowly oblong (5) oblong-narrowly oblong (6), oblong (7), oblanceolate (8)
21.	leaf shape at the set apex	Not observed (0), narrowly oblong (1), narrowly elliptic (2), elliptic (3), elliptic-narrowly elliptic (4)
22.	leaf margins	Entire (0), ciliate as it young and entire as it mature (1)
23.	leaf base in a flushing set	Varied (0), patterned (1), uniform (2)
24.	leaf base at the set base	Cuneate-obtuse (0), cuneate (1), obtuse (2), emarginate (3), truncate (4), attenuate (5)
25.	leaf base at the middle set	Rounded (0), cuneate-obtuse (1), cuneate (2), cuneate-rounded (3), emarginate (4), truncate (5), attenuate (6)
26.	leaf base at the set apex	Obtuse (0), cuneate-obtuse (1), cuneate (2), emarginate (3), truncate (4), attenuate (5)
27.	leaf apex in a flushing set	Varied (0), patterned (1), uniform (2)
28.	leaf apex at the set base	Acute (0), acuminate-acute (1), mucronulate (2), acuminate (3), retuse (4), acute/retuse (5)
29.	leaf apex at the middle set	Acute (0), acuminate-acute (1), acuminate (2), acute-rounded (3)
30.	leaf apex at the set apex	Acute (0), acuminate-acute (1), acuminate (2), obtuse (3)
31.	leaf veins	Eucamptodromous (0), hyphodromous (1), brochidodromous (2), cladodromous (3)
32.	adaxially vein	Invisible (0), visible (1)

Table 1. Morphological characters for the phenetic analysis (Continue)

No	Characters	Character set (code)
33.	abaxially vein	Invisible (0), visible (1)
34.	adaxially midvein indumentum closure	Glabrous (0), glabrescent (1), puberulous (2)
35.	abaxially midvein indumentum closure in a flushing set	Patterned (0), uniform (1)
36.	abaxially midvein indumentum closure	Glabrous (0), glabrescent (1), glabrescent-glabrous, glabrescent on the base and glabrous on the apex of set (2), puberulous (3)
37.	abaxially leaf surface indumentum closure in a flushing set	Patterned (0), uniform (1)
38.	abaxially leaf surface indumentum closure	Glabrous (0), glabrescent (1), glabrescent-glabrous, glabrescent on the base and glabrous on the apex of set (2), puberulous (3)
39.	adaxially leaf surface indumentum closure	Glabrous (0), glabrescent (1)

servation, petiole length, the angle between the petiole and the twig, and the size of the lamina were measured.

Data Analysis

Data obtained from observations were analized descriptively to explain the morphological development of leaf flushing, its phenology, morphological variations, and to compose species descriptions and determination key. The coefficient of similarity was analized by SIMQUAL using the cofficient of Hamann (H), Roger & Tanimoto (RT) and simple matching (SM). Clustering analysis was analized using SAHN by the UPGMA, WPGMA, complete-link and single-link. Cophenetic correlation coefficients (r) were calculated using COPH and MCOMP. The best combination (Rohlf 1998) was then used to produce a dendrogram using TREE. Principal coordinate analysis (PCO) was performed using the procedures DCENTER, EIGEN and MXPLOT. All of them were performed by NTSYSpc version 2.11a.

RESULTS AND DISCUSSION

Morphological Development

D. blancoi was used as a representative model for the general leaf flushing of morphological development of *Diospyros* (Figure 1). Leaf flushing was preceded by the formation of an early bud which is turning into a dormant bud. A dormant bud is the part of twigs connected to the pith by a bud trace, modified by an encased growth which may later be stimulated to sprout, externally characterized by the slowing down and finally ending of internode expansion of primordias within it (Kozlowski 1971). The term of bud dormancy for woody plants of the Temperate Zone are known as temporary growth suspension during the winter (Kozlowski 1971). Dormancy in this study means the rest period of growth which is externally characterized by the constant size of bud and no morphological alteration.

After a dormant period, the dormancy of the bud was broken. The end of the bud dormancy can be identified by the falling down of the outermost cataphyll or the abrupt increase of bud size. After all cataphylls have fallen, the foliage leaves expand from the bud sequentially based on their age. A new apical early bud will have already formed when the last leaf has expanded from the preceding dormant bud.

Bud development produced a twig with flushing sets (Figure 1F, Figure 7). The flushing set is the part of the twig and their leaves that were produced from the same dormant bud. The part of the twig near the first expanded leaf is named the base of the flushing set. Whereas, the part of the twig near the position of the last leaf to expand, exactly before the subsequent early bud has formed, is named the apex of the flushing set.

The division of axis length was known in seedlings and saplings of *Notophagus alpina* as growth unit or GU (Puntieri *et al* 2007). It was state that the size of GU was more closely related to the number of foliage leaves than to the number of cataphylls. However, it may be confused with the term of stem unit growth that was proposed by Meicenheimer (2006). Growth unit introduced by Puntieri *et al* (2007) means an axis portion developed in one uninterrupted extension event just like the term of flushing set in this study. Whereas, growth unit introduced by Meicenheimer (2006) means phytomer unit, especially the arrangement of node and internode.

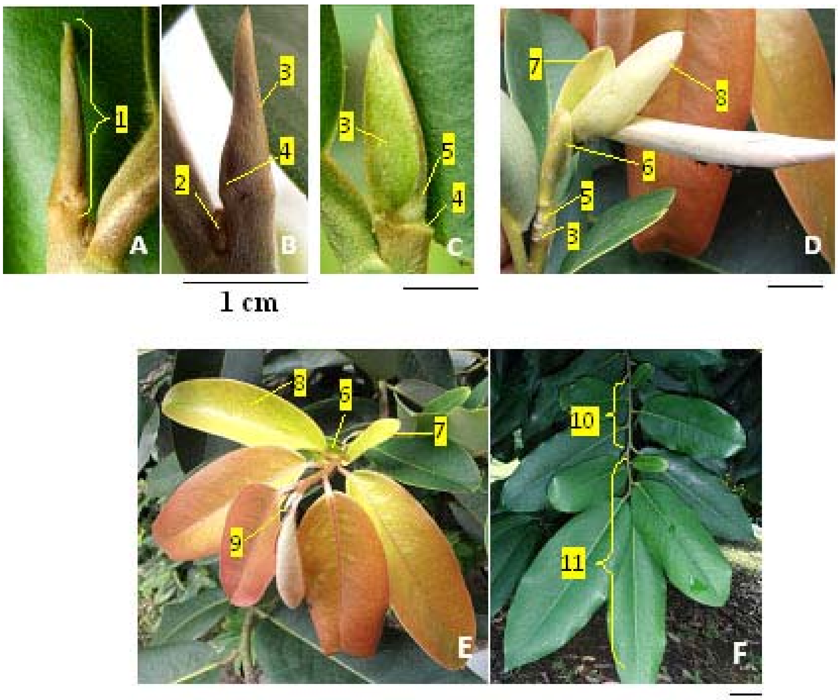

Figure 1. Leaf flushing morphological development of *D. blancoi*. [A] early bud; [B] dormant bud; [C] bud break, outermost cataphyll has fallen; [D] all cataphylls have fallen, foliage leaves were expanding from the bud; [E] new early bud already formed when the last young leaf in a flushing set expanding from the bud; [F] mature flushing set. [1] apical bud; [2] axillary bud; [3] 1st cataphyll; [4] 2nd cataphyll; [5] 3rd cataphyll; [6] 1st foliage leaf; [7] 2nd foliage leaf; [8] 3rd foliage leaf; [9] early bud; [10] 1st flushing set; [11] 2nd flushing set.

The flushing leaves were soft and hung down from the twigs. Each petiole formed an acute angle with the twigs (Figure 2A). As the leaves grew older, the lamina became more rigid and extensive with adaxial surface facing up the sunlight. Each petiole formed a bigger angle with the twigs (Figure 2B). Young leaves were reddish or pale green and became dark green when it matured. The changing of colour started from the leaf near the flushing set base to the set apex and from the nearest part of midvein to the leaf margins (Figure 1E). As the leaves matured, no more alteration were found.

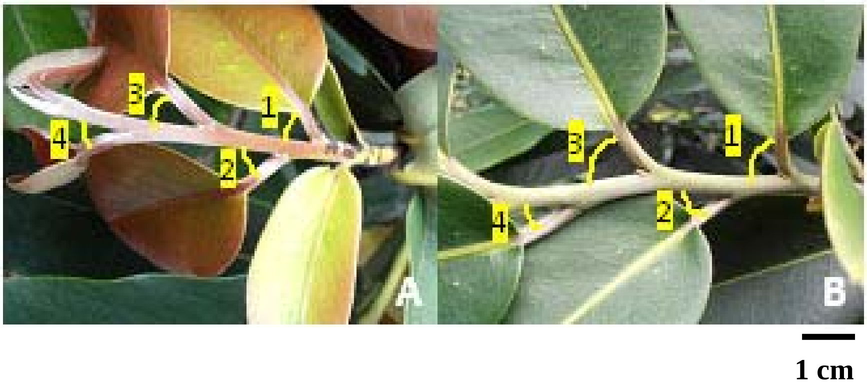

Figure 2. The angle between petioles and twigs in *D. blancoi*. [A] young leaves; [1] 50^0; [2] 40^0; [3] 40^0; [4] 35^0. [B] mature leaves; [1] 80^0; [2] 45^0; [3] 65^0; [4] 35^0.

Young leaves are lack toughness because the toughness is provided by cell-wall thickening and lignification which tend to be incompatible with cell expansion and leaf growth (Lambers 2008). The colour of red in young leaves is caused by the accumulation of anthocyanins and has some advantages, i.e. the protection from insect herbivory and excess light (Dominy *et al* 2002; Karageorgou & Manetas 2005; Lambers 2008).

Bud scales or cataphylls, that protected the bud from water lost, might be the overlapped stipules or modified leaves (Wareing & Philips 1970). Cataphylls of *Diospyros* were some of the outermost leaf primordias of the bud which were modified and enclosed the shoot apex. Even they have a leaf-like structure at the early development, their lamina development was suppresed during the development of the bud because of the arrested growth (Wareing & Philips 1970). Cataphylls were overlapped, tightly fitted to the base of bud and left the flushing set without becoming a foliage leaf (Corner 1964). Cataphylls fall sequentially based on their age and leave scars on the twig. These scars can usually be used as an identified value for the base of the flushing set.

The number of cataphylls and foliage leaves in a flushing set were varied for each flushing set of species observed, even for the flushing sets from the same twig. Preliminary study by Romberger (1963) stated that primordia were not predestined to form scales or leaves and were capable of becoming either of these. It was stated that the existing environmental condition play a role for their morphogenic determination at an early developmental stage. Kozlowski (1971) stated that unfavourable environment lead the leaf primordia developed into scales instead of foliage leaves. He stated that cataphyll primordium is indistinguishable from foliage leaf primordium but cataphyll tissues developed more rapidly than the foliage leaf but show less differentiation so that the vascular system and mesophyll are weakly developed, the stomates are infrequent or lacking.

The first expanded leaf of *D. blancoi* and *D. jaherii* flushing sets have a much smaller size than other leaves. Romberger (1963) said that cataphylls and foliage leaves often differ only in degree because there are various intermediate stages and gradual transition in development between both of them. This small reduced leaf may be the intermediate stages between cataphyll and foliage leaf. Even after becoming a foliage leaf, this small leaf has been reduced and indicates their arrested growth at the time of bud growth.

Phenology

All species of *Diospyros* observed had a rhythmic growth. The bud did not continue to add new leaves to produce a shoot but showed growth intermittency due to bud dormancy. This fact confirms the preliminary study that alternation of growth and bud dormancy found in tropical as in temperate trees (Borchert 2000; Yanez-Espinosa 2006) and contradicted the theory that tropical trees usually showed continuous growth throughout their life cycle (Kozlowski 1971).

The flushing period indicated the presence of an arrested growth in the bud. The time required for a bud to expand all of its young leaves was 15–25 days and for the mature leaves formed was 40–55 days (Table 2). The leaf flushing phenology of *D. pilosanthera* could not fully be observed due to the attacks of insects and fungi.

Table 2. Leaf Flushing Phenology

No	Species	Time to bud break	Completion time for all foliage leaves to expand*	Completion time for mature flushing set *
1.	*D. malabarica*	March-April, October-November	10–15	40–50
2.	*D. beccarioides*	March, May-June, September	Not observed	Not observed
3.	*D. buxifolia*	June-July, October-December	15–21	35–50
4.	*D. jaherii*	All the time, especially November-December	18–25	40–45
5.	*D. blancoi*	March-June, September-December	25–30	45–55
6.	*D. celebica*	March, June-July, October-early December	20–25	40–45
7.	*D. cauliflora*	April-June, October-December	21–30	50–60
8.	*D. pilosanthera*	June, September-early October	Not observed	Not observed

* days after bud break

Generally, *Diospyros* young leaves is found every few months but *D. jaherii* young leaves is found throughout the year with the most flushing leaves found on November-December. Tropical species usually have no real seasonal aspect contrasted strongly with the relatively short burst of shoot growth followed by a long period of bud dormancy of many Temperate Zone trees (Kozlowski 1971). *D. jaherii* has no real seasonal aspects just like ordinary tropical plant. On the contrary, most species of *Diospyros* showed seasonal shoot growth just like Temperate Zone trees though their shoot growth were more intermittent and occupies more of the year.

Seasonal production of foliage leaves might be once a year or continue to add new leaves, either by a continuous growth or by reccurent flushing (Kozlowski 1971). Based on the observation results made by Holltum in Garden's Bulletin Singapore, Kozlowski (1971) reported that the period of shoot growth were varied for 6 months, 6 to 12 months, 12 months, greater than 12 months or no regular period. Most of *Diospyros* species observed have a reccurent flushing with no regular period of shoot growth. Their shoot growth involved the elongation of more than one terminal bud per shoot each year.

The time of bud broken was not simultaneous in all *Diospyros* species, all individual trees within the same species, even in all buds of an individual tree under similar external condition. Shoots of the same tree often show different growth pattern because of their different stages of development (Kozlowski 1971). The time of bud broken was affected by some external and internal factors. External factors that affected bud broken time were temperature, photoperiodism, mineral availibility, and water supply (Kozlowski 1971). Bud broken time was controlled internally by the phase of dormancy and the balance between endogenous hormone, i.e. absisic acid as growth inhibitors and gibberelin as growth promoters (Vegis 1963; Kozlowski 1971). A dormant bud has three possibilities of broken when exposed to the favourable environmental condition according to its dormancy phase, i.e. 1) bud break begins later and takes a longer time than usual at the beginning of the rest period (predormancy) because of a decreasing growth activity so that the bud does not always succeed in reacting to the favourable environmental condition, 2) no bud break takes place in at the middle rest period (true dormancy), 3) nearly all the buds break at the after-rest period because of the maximal possible level of growth activity (Vegis 1963).

Borchert (2000) stated dry season synchronize growth in tropics by the changes in tree water balance. He also stated that bud break of evergreen species usually occurs during the early or mid-dry season. Although classified as evergreen, *Diospyros* observed did not show such growth pattern. Secondary data including monthly temperature, rain fall and air humidity showed that there were no significant environmental changes in the year 2012. There was also no real dry season in the year 2012, so the seasonal growth observed was not mainly affected by environmental condition. Therefore, it confirms the preliminary information that seasonal growth in trees can be found in non-seasonal environments (Killmann & Hong 1955).

Morphological Variation

Leaf characters that have been used for *Diospyros* identification was confined to mature leaf characters (Ridley 1923; Bakhuizen van den Brink 1936; Backer & Bakhuizen van den Brink 1965; Corner 1988). Instead of mature leaf characters, *Diospyros* leaf flushing also provided bud, young leaf and flushing set characters.

Bud Characters

Vernation of all *Diospyros* observed were equitant (Figure 3). Variation of bud characters included the early and dormant bud colour, the length of dormant bud, indumentum closure and colour of early and dormant bud. It also included the presence, the number of cataphyll, and the presence of dorsal cataphyll.

Figure 3. *Diospyros* vernation.

The colour of the early and dormant bud might be the same or has changed in line with their dormancy time (Figure 4). The bud of *D. buxifolia, D. jaherii, D. blancoi* and *D. celebica* were brown with silvery-brown indumentum. The early bud of *D. malabarica, D. beccarioides, D. cauliflora* were green with white indumentum and changed into black when it turned dormant. The early bud of *D. pilosanthera* was green and became brown when it turned dormant.

The length of the dormant bud (Figure 4) was less than 0,5 cm for *D. buxifolia* and *D. jaherii*, 0,6–0,9 cm for *D. cauliflora* and *D. pilosanthera*, or more than 1 cm for other *Diospyros*. Bud indumentum were glabrous (not hairy) for *D. pilosanthera*, sericeous (silky) for *D. blancoi* and *D. celebica*, or pubescent (short soft hair, downy) for other *Diospyros*.

Cataphylls were found in most *Diospyros* observed, but sometimes absent in *D. buxifolia*. The number of cataphylls were various, i.e. one for *D. beccarioides* and more than 1 for other *Diospyros*. Dorsal cataphylls were only found in *D. jaherii*.

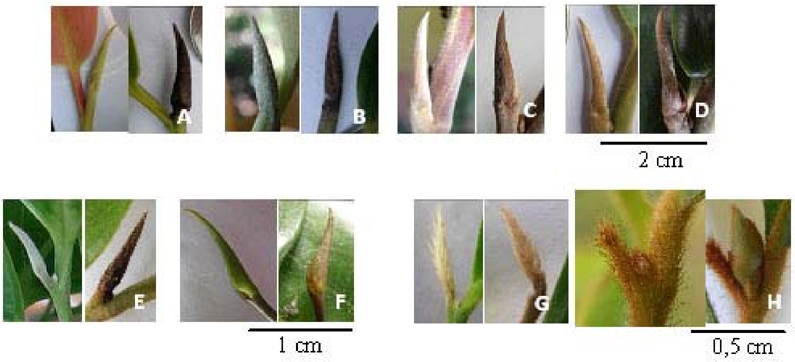

Figure 4. *Diospyros* early bud (the left side) and dormant bud (the right side). [A] *D. malabarica*; [B] *D. beccarioides*; [C] *D. blancoi*; [D] *D. celebica*; [E] *D. cauliflora*; [F] *D. pilosanthera*; [G] *D. buxifolia*; [H] *D. jaherii*.

Young Leaves

Variation of young leaf characters included the colour and ptyxis (Figure 5). Young leaves colour were reddish for *D. malabarica* and *D. beccarioides*, pale green or reddish for *D. blancoi*, and pale green for other *Diospyros*. Ptyxis were involute (margin rolled adaxially) for *D. malabarica*, *D. beccarioides*, *D. blancoi*, and *D. celebica,* conduplicate (lamina folded adaxially) for *D. buxifolia* and *D. cauliflora,* curved (lamina curved in an arc) for *D. jaherii*, or revolute (margin rolled abaxially) for *D. pilosanthera*.

This study showed that the characters of young leaves were varied and potential for of *Diospyros* observed. It can be used to confirm that these characters were potential for identification as mentioned before (Balgooy 1977; Cullen 1978).

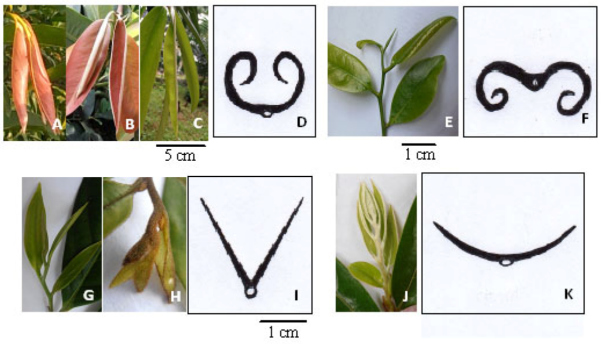

Figure 5. Young leaves and ptyxis of *Diospyros*. Ptyxis of *D. malabarica* [A]; *D. blancoi* [B] and *D. celebica* [C] are named involute [D]; *D. pilosanthera* [E] named revolute [F]; *D. cauliflora* [G] and *D. buxifolia* [H] named conduplicate [I]; *D. jaherii* [J] named curved [K].

Mature Leaves

The number of *Diospyros* foliage leaves in a flushing set were 3–20 and arranged alternately. Characters of the mature leaf included phytomer characters (leaf size, internodus length and petiole length), leaf shape, leaf base, leaf apex, leaf margin, leaf vein type and their visibility on adaxial and abaxial surface, indumentum closure of petiole, abaxially and adaxially indumentum closure of midvein, and abaxially and adaxially indumentum closure of leaf surface (Table 3).

Table 3. Character variations of *Diospyros* mature leaves

Character/Taxon	*D. malabarica*	*D. beccarioides*	*D. buxifolia*	*D. jaherii*	*D. blancoi*	*D. celebica*	*D. cauliflora*	*D. pilosanthera*
Leaf shape in a flushing set	base set elliptic-lanceolate, narrowly oblong to the set apex	narrowly elliptic	elliptic-narrowly elliptic	set base elliptic-circular; middle set narrowly oblong; set apex narrowly elliptic	set base elliptic, oblong-narrowly oblong or elliptic-narrowly elliptic to the set apex	set base narrowly elliptic, middle set narrowly oblong, narrowly elliptic-narrowly oblong at the set apex	set base narrowly elliptic-oblanceolate, middle set oblanceolate, set apex narrowly elliptic	unobserved
Leaf base in a flushing set	set base cuneate-obtuse, middle set rounded, set apex obtuse	cuneate-obtuse	cuneate	base set obtuse, cuneate to set apex	obtuse-rounded or emarginate	emarginate or truncate	cuneate	attenuate
Leaf apex in a flushing set	acute	acuminate-acute	acute	base set mucronulate, acuminate to the set apex	base set mucronulate, acute-acuminate to the set apex	base set mucronulate, acute-acuminate to the set apex	acuminate	acute-rounded
Petiole	patterned	patterned	puberulous	puberulous	glabrescent	puberulous	patterned	glabrous
Abx midvein	patterned	patterned	puberulous	puberulous	glabrescent	puberulous	patterned	glabrous
Abx leaf surface	patterned	glabrous	puberulous	glabrescent	glabrescent	glabrescent	glabrescent	glabrous
Adx midvein	glabrous	glabrous	glabrescent	puberulous	glabrous	glabrous	glabrous	glabrous
Adx leaf surface	glabrous	glabrous	glabrescent	glabrous	glabrous	glabrous	glabrous	glabrous
Leaf margin	entire	entire	ciliate becoming entire	ciliate becoming entire	ciliate becoming entire	ciliate becoming entire	entire	entire
Leaf vein	eucamptodromous	eucamptodromous	hyphodromous	brochidodromous	brochidodromous	cladodromous	cladodromous	cladodromous
Leaf vein visibility	adx, abx	adx, abx	none	adx, abx	adx	adx	adx, abx	adx, abx

Note: patterned means glabrescent at the base and glabrous at the set apex; abx means abaxially; adx means adaxially.

Diospyros phytomer characters in a flushing set were patterned, except *D. buxifolia* which was uniform (Fig. 6). Phytomer characters are well known in clover plant (Aitken 1974). She stated that each successive phytomer, included width of node, length of petiole and length of leaflet, on the young shoot tends to be larger than the previous one. The pattern of phytomer characters in a flushing set was explored for the first time in this study.

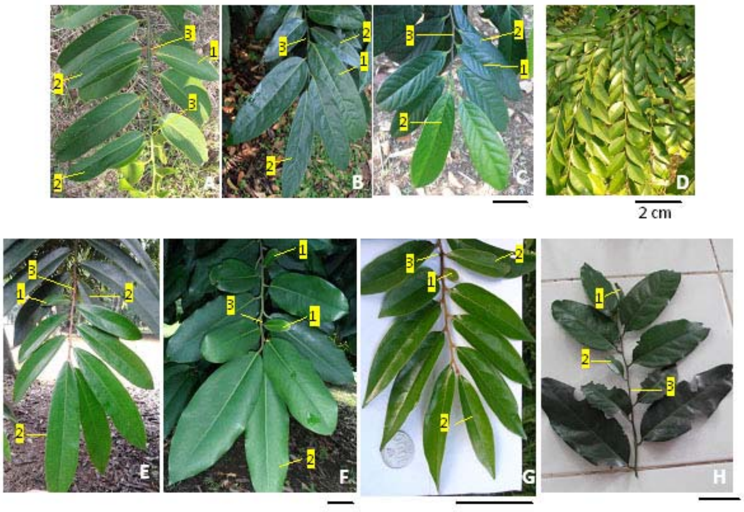

Figure 6. *Diospyros* flushing set. [A] *D. malabarica*; [B] *D. beccarioides*; [C] *D. cauliflora*; [D] *D. buxifolia*; [E] *D. celebica*; [F] *D. blancoi*; [G] *D. jaherii*; [H] *D. pilosanthera*. [1] foliage leaf nearby the base of flushing set; [2] foliage leaf nearby the apex of flushing set; [3] cataphyll scar.

The pattern of internodus length and petiole length in a flushing set were enlarged from the base to the middle set and smaller to the set apex. The pattern of the leaf size in a flushing set of *D. jaherii* was enlarged from the base to the middle set and the same size to the set apex or sometimes smaller only on its apex, *D. blancoi* and *D. celebica* were enlarged to the set apex or smaller only on its set apex, and other *Diospyros* were enlarged from the base to the middle set and smaller to the set apex. Leaf size distribution of *D. pilosanthera* was not observed because their flushing set with intact and complete mature leaves were very rare due to the attacks of insects and fungi.

The terminology of leaf shape, leaf base, and leaf apex in a flushing set were uniform, patterned or varied (Table 3). Uniform means that all foliage leaves in a flushing set have the same terminology. Patterned and varied means that the terminology of all foliage leaves in a flushing set varies. Patterned means that the variation has a pattern, whereas varied has no pattern.

Leaf shape were uniform in *D. beccarioides*, varied in *D. buxifolia*, or patterned in other *Diospyros*. Leaf bases were varied in *D. beccarioides* and *D. blancoi*, patterned in *D. malabarica* and *D. jaherii*, and uniform in other *Diospyros*. Leaf apexes were uniform in *D. jaherii*, *D. blancoi* and *D. celebica*, varied in *D. beccarioides* and *D. pilosanthera*, or patterned in other *Diospyros*.

Flushing Set

A flushing set of *Diospyros* can be distinguished from the previous one by the presence of cataphyll scars on the twig (Fig. 7), except on *D. buxifolia* which were sometimes absent of cataphyll (Fig. 8). A flushing set without cataphylls was very difficult to be ascertained, except they had a pattern in the characters of their phytomer. This pattern was not found in *D. buxifolia*. Though it had cataphyll, the flushing set of D. *buxifolia* was still difficult to be distinguished. The cataphylls had a very small size (0,3 cm). Therefore, the scars on the twig were no longer visible after the twig became woody (Fig. 9).

Foliage leaf near the flushing set base of *D. blancoi* and *D. jaherii* was reduced and much smaller than other normal leaves in a flushing set. This small leaf can be used as an additional value to distinguish a flushing set from the previous one.

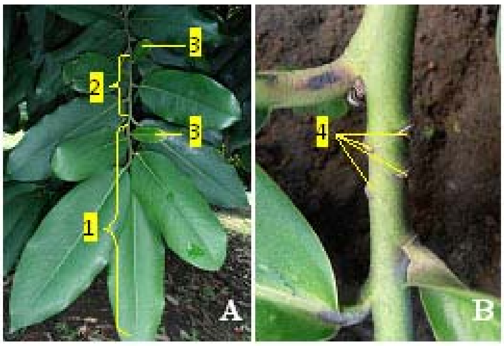

Figure 7. Flushing set of *D. blancoi*. [1] 1st flushing set; [2] 2nd flushing set; [3] small reduced leaf; [4] cataphyll scars at the flushing set base.

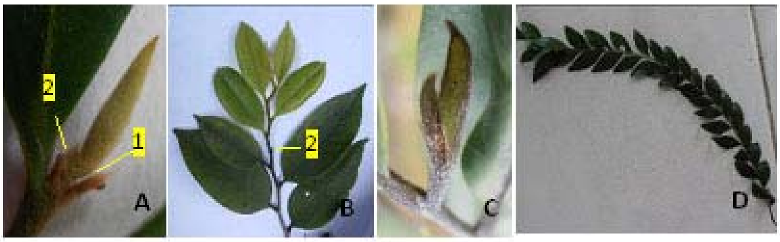

Figure 8. Bud and flushing set of *D. buxifolia*. [A] Bud with cataphyll; [B] flushing set with cataphyll; [C] bud without cataphyll; [D] flushing set without cataphyll. [1] aborted apical bud; [2] cataphyll scar.

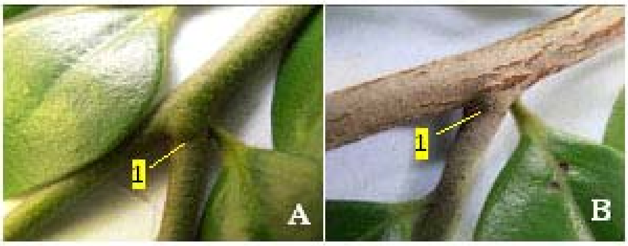

Figure 9. Invisible cataphyll scar of *D. buxifolia* when the twigs become woody. [A] Twigs before becoming woody; [B] after becoming woody. [1] cataphyll scar.

Taxonomic Implication

The variations of characters provided by leaf flushing of eight species of *Diospyros* studied seems to be constant. Therefore, it is possible to characterize the species by delimitation and circumscribing each one of them by the leaf flushing characters. Consequently, it is also possible to construct a determination key to identify the species studied based solely on the leaf flushing characters.

Key to *Diospyros* spp. Using Leaf Flushing Characters

1. a. Early bud brown, indumentum of the early and dormant bud silver-brown 2
b. Early bud green, indumentum white or none, indumentum of dormant bud black or none 5
2. a. Flushing set distinguishable. Leaf apex, length of petioles and internodus in a flushing set patterned. Leaf vein eucamptodromous, brochidodromous or cladodromous; adaxially midvein indumentum glabrous or puberulous; abaxially leaf surface glabrescent, adaxially glabrous 3
b. Flushing set indistinguishable. Leaf apex, length of petioles and internodus in a flushing set uniform. Leaf vein hyphodromous; adaxially midvein indumentum glabrescent; abaxially leaf surface pubescent, adaxially glabrescent ....*D. buxifolia*
3. a. Early and dormant bud indumentum sericeous. Dormant bud ≥ 1 cm. Dorsal cataphyll absent. Ptyxis involute; adaxially midvein indumentum glabrous 4

b. Early and dormant bud indumentum pubescent. Dormant bud ≤ 0,5 cm. Dorsal cataphyll present. Ptyxis curved; adaxially midvein indumentum puberulous .... *D. jaherii*

4\. a. Leaf shape oblong-elliptic, leaf veins brochidodromous. Indumentum of petioles and abaxially midvein glabrescent .... *D. blancoi*

b. Leaf shape narrowly oblong-narrowly elliptic, leaf veins cladodromous. Indumentum of petioles and abaxially midvein puberulous .... *D. celebica*

5\. a. Early and dormant bud pubescent. Dormant bud black. Ptyxis conduplicate or involute. Leaf base cuneate, obtuse or rounded. Abaxially midvein indumentum in a flushing set patterned, glabrescent at the flushing set base, glabrous at the set apex 6

b. Early and dormant bud glabrous. Dormant bud brown. Ptyxis revolute. Leaf base attenuate. Abaxially midvein indumentum in a flushing set uniform, glabrous ....*D. pilosanthera*

6\. a. Dormant bud 1–2 cm. Young leaves reddish, ptyxis involute. Leaf vein eucamptodromous 7

b. Dormant bud 0,6–0,9 cm. Young leaves pale green, ptyxis conduplicate. Leaf vein brochidodromous .... *D. cauliflora*

7\. a. Cataphyll > 1. Leaf shape in a flushing set patterned, narrowly elliptic or lanceolate at the set base, narrowly oblong to the set apex. Abaxially leaf surface indumentum in a flushing set patterned, glabrescent at the set base, glabrous at the set apex .... *D. malabarica*

b. Cataphyll always 1. Leaf shape in a flushing set uniform, narrowly elliptic. Abaxially leaf surface indumentum in a flushing set uniform, glabrous .... *D. beccarioides*

Phenetic Analysis

The cophenetic correlation coefficient obtained was more than 0,90 (Table 4) which indicates that the quality of fit for all combinations of the similarity matrix and cluster analysis was very good (Rohlf 1998). Therefore, all the combinations were appropriate to be used in analyzing the phenetic relationship. Among the cluster methods, UPGMA yielded the highest cophenetic correlation and identical tree topologies for all similarity index. Cophenetic correlation of combination of UPGMA and the Roger & Tanimonto yielded the highest cophenetic correlation (Table 4). It was considered as the most suitable combination for data analysis.

Table 4. Cophenetic correlation coefficients of eight *Diospyros* species observed

Clustering/Similarity*	SM	RT	H
UPGMA	0,95	0,98	0,95
WPGMA	0,95	0,97	0,95
COMPLETE-LINK	0,94	0,97	0,94
SINGLE-LINK	0,94	0,97	0,94

* UPGMA, unweighted pair group method with arithmetic means; WPGMA, weighted pair group method with arithmetic means; SM, simple matching coefficient; RT, Rogers and Tanimoto's distance; H, Hamann's coefficient.

Two groups were formed at the coefficient of similarity of 33% (Figure 10). Group I contained *D. malabarica, D. beccarioides, D. cauliflora,* and *D. pilosanthera*. Group II contained *D. buxifolia, D.jaherii, D. blancoi,* and *D. celebica.* They were separated from the others by the colour of the early bud, indumentum colour of the early and dormant bud, the distribution of leaf size in a flushing set, leaf margin, and indumentum closure of petiole and abaxially midvein.

The most similar species in group I were *D. malabarica* and *D. beccarioides* (Appendix 1). They were grouped by the number of cataphylls, leaf shape, leaf base and leaf apex in a flushing set, and indumentum closure of abaxially leaf surface. *D. cauliflora* and *D. pilosanthera* were joined with them at the coefficient of similarity of 56% and 37% respectively.

The most similar species in group II were *D. blancoi* and *D. celebica* (Appendix 1). They were grouped by leaf shape in set base and middle part, leaf vein, and indumentum of petioles and abaxially midvein. Both of them were the same taxon in subgenus *Eudiospyros* (L.) Bakh., section *Ebenaster* Bakh. based on their generative similar characters, i.e. infloresence, calyx, corolla, stamen and fruit (Bakhuizen van den Brink 1936). *D. jaherii* and *D. buxifolia* were joined with them at coefficient of similarity 55% and 35% respectively.

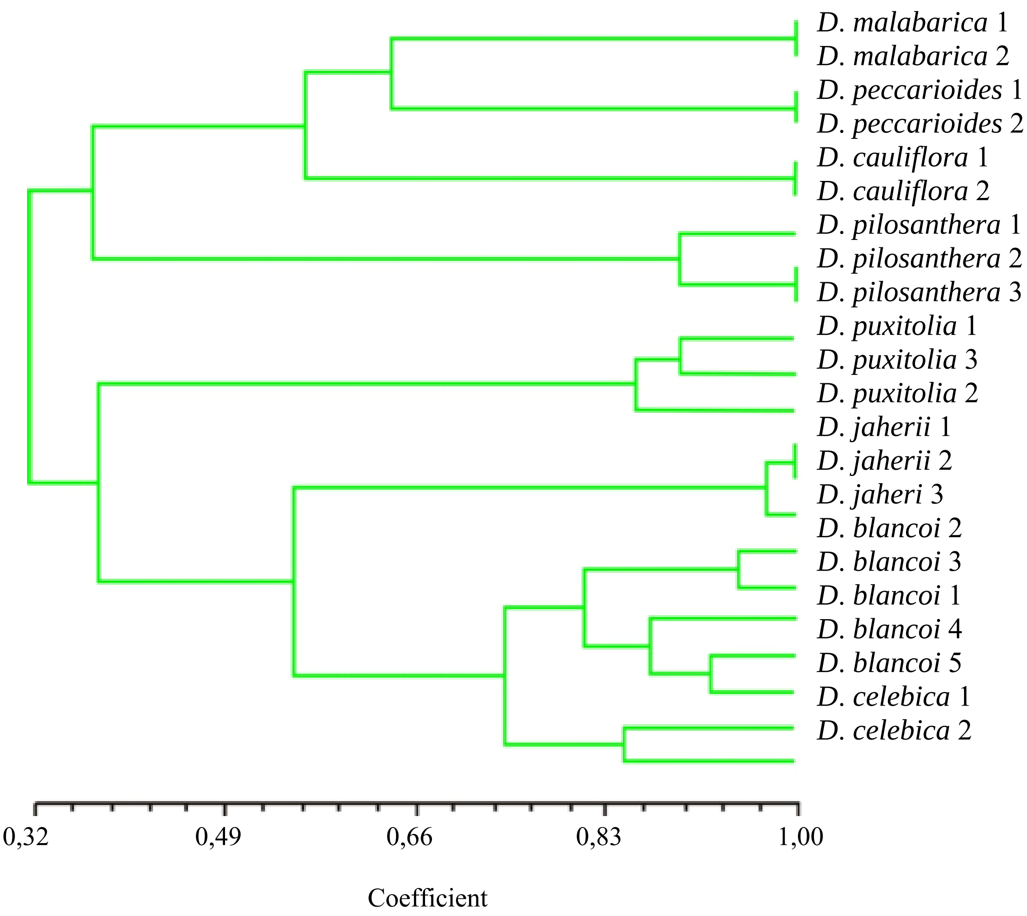

Figure 10. Dendrogram of 22 *Diospyros* individual trees: Rogers & Tanimoto distance, UPGMA clustering.

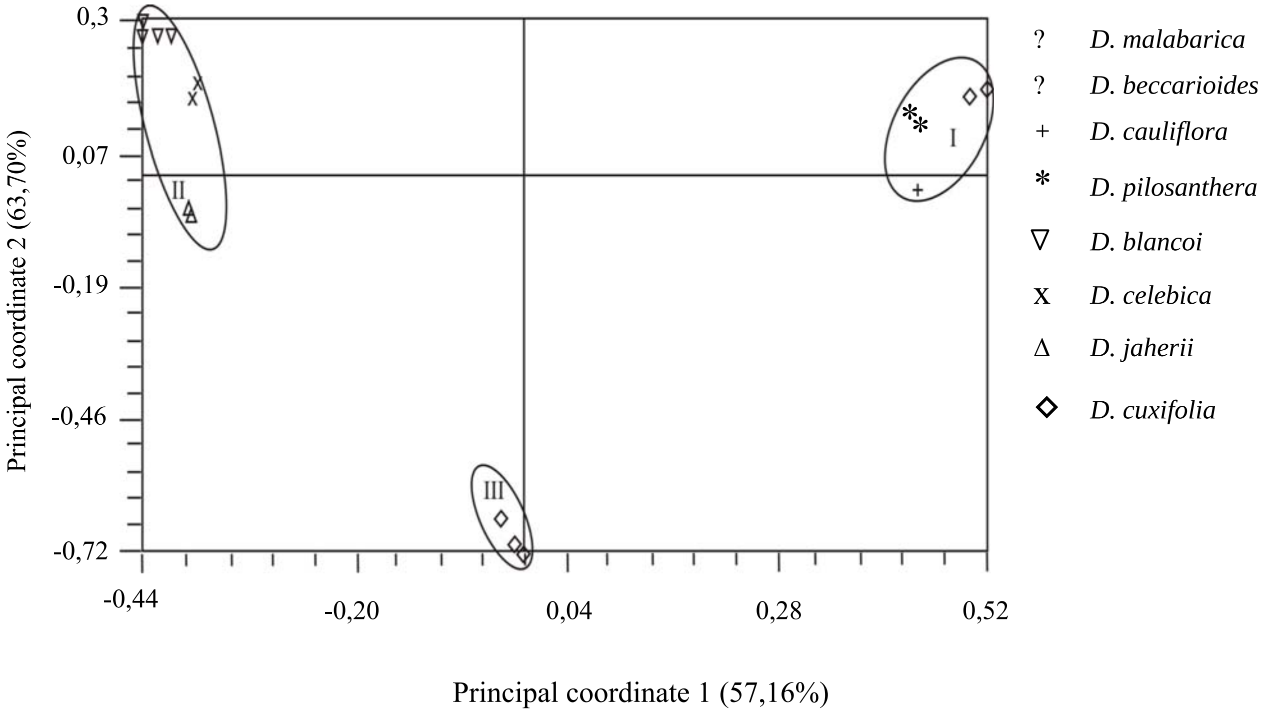

Figure 11. Principal coordinate analysis of 22 individual trees of *Diospyros*: Rogers & Tanimoto distance, UPGMA clustering.

The results of PCO analysis showed that the first two axes accounted for 15.49% and 11.29% of the data variance (Figure 11). The first axes was formed by two characters, i.e. the colour of dormant bud and abaxial midvein indumentum closure in flushing set. Whereas, the second axes was formed by adaxially midvein indumentum closure. Leaf indumentum closure was confirmed before as an heritable characters associated with pronounced variation in *Encelia farinosa* (Housman *et al* 2002). There is no record about the usage of the colour of dormant bud character.

Cumulatively, the PCO results represented 26.79% of the data, which were sufficient to resolve all the observed individual trees into three distinct groups. Group I contained *D. malabarica, D. beccarioides, D. cauliflora* and *D. pilosanthera*. Group II contained *D. jaherii, D. blancoi* and *D. celebica*. Group III contained *D. buxifolia*.

The PCO analysis showed that *D. jaherii* was not grouped together with *D. buxifolia* eventhough they were included in the same section, i.e. section *Brachycylix* Bakh. (Bakhuizen van den Brink 1936). *D. jaherii* was grouped into group II together with section *Ebenaster* Bakh. (*D. blancoi* and *D. celebica*). This was because *D. jaherii* has more leaf flushing similarity characters to the group II than *D. buxifolia*. The similar characters between *D. jaherii* and *D. buxifolia* included indumentum closure of early bud and dormant bud, the length of dormant bud, indumentum closure of petiole, and leaf base in the set apex. The similar characters among *D. jaherii*, *D. blancoi* and *D. celebica* were included the flushing set, the present and number of cataphyll, internodus length, leaf shape in a flushing set, leaf base in a flushing set, leaf apex in a flushing set, leaf vein, visibility of adaxially vein, and indumentum closure of adaxially and abaxially leaf surface.

CONCLUSION

Bud development of *Diospyros* involves a rhythmic growth and produces flushing sets. Flushing set are usually distinguished from the previous one by cataphyll scars, the pattern of the phytomer characters and the presence of small leaf in some species. The flushing time after a period of bud dormancy and the presence of small leaf indicates that arrested growth have taken place in the form of buds. *Diospyros* have seasonal shoot growth patterns similar to the Temperate Zone trees, except *D. jaherii*. Characters of bud, young leaf, mature leaf, and flushing set can be used to identify *Diospyros* species observed. Dendrogram shows that 22 individual trees of *Diospyros* observed can be clustered by leaf flushing characters according to their species at the similarity coefficient of 76% and a very good cophenetic correlation (r = 0.98). Thus, leaf flushing provides characters as taxonomic evidence of the eight *Diospyros* species observed.

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Appendix 1. Index similarity of 22 individual trees of *Diospyros*

```
                     D._malab D._malab D._becca D._becca D._buxif D._buxif
                    ------------------------------------------------------------
D._malabarica_1     | 1.0000
D._malabarica_2     | 1.0000   1.0000
D._beccarioides_1   | 0.6410   0.6410   1.0000
D._beccarioides_2   | 0.6410   0.6410   1.0000   1.0000
D._buxifolia_1      | 0.2051   0.2051   0.1538   0.1538   1.0000
D._buxifolia_2      | 0.2308   0.2308   0.1538   0.1538   0.9231   1.0000
D._buxifolia_3      | 0.2308   0.2308   0.1538   0.1538   0.8974   0.9487
D._jaherii_1        | 0.2564   0.2564   0.2821   0.2821   0.3590   0.3846
D._jaherii_2        | 0.2564   0.2564   0.2821   0.2821   0.3590   0.3846
D._jaherii_3        | 0.2564   0.2564   0.2564   0.2564   0.3846   0.4103
D._blancoi_1        | 0.3333   0.3333   0.3333   0.3333   0.2821   0.3333
D._blancoi_2        | 0.3333   0.3333   0.3077   0.3077   0.3077   0.3077
D._blancoi_3        | 0.3077   0.3077   0.2821   0.2821   0.3333   0.3333
D._blancoi_4        | 0.4103   0.4103   0.3590   0.3590   0.3333   0.3590
D._blancoi_5        | 0.4103   0.4103   0.2821   0.2821   0.3590   0.3590
D._celebica_1       | 0.2821   0.2821   0.3333   0.3333   0.3590   0.3846
D._celebica_2       | 0.3590   0.3590   0.3077   0.3077   0.4103   0.4103
D._cauliflora_1     | 0.5641   0.5641   0.5641   0.5641   0.3077   0.3333
D._cauliflora_2     | 0.5641   0.5641   0.5641   0.5641   0.3077   0.3333
D._pilosanthera_    | 0.3077   0.3077   0.3590   0.3590   0.1795   0.1795
D._pilosanthera_    | 0.3590   0.3590   0.3333   0.3333   0.2308   0.2308
D._pilosanthera_    | 0.3590   0.3590   0.3333   0.3333   0.2308   0.2308


                     D._buxif D._jaher D._jaher D._jaher D._blanc D._blanc
                    ------------------------------------------------------------
D._buxifolia_3      | 1.0000
D._jaherii_1        | 0.3590   1.0000
D._jaherii_2        | 0.3590   1.0000   1.0000
D._jaherii_3        | 0.3846   0.9744   0.9744   1.0000
D._blancoi_1        | 0.2821   0.5897   0.5897   0.5897   1.0000
D._blancoi_2        | 0.2821   0.5128   0.5128   0.5128   0.8462   1.0000
D._blancoi_3        | 0.3077   0.5385   0.5385   0.5385   0.8205   0.9487
D._blancoi_4        | 0.3077   0.5385   0.5385   0.5385   0.8974   0.7949
D._blancoi_5        | 0.3333   0.5385   0.5385   0.5385   0.8462   0.8205
D._celebica_1       | 0.3846   0.6154   0.6154   0.6154   0.7436   0.7436
D._celebica_2       | 0.4359   0.5385   0.5385   0.5385   0.6667   0.7949
D._cauliflora_1     | 0.3077   0.4359   0.4359   0.4615   0.3846   0.3846
D._cauliflora_2     | 0.3077   0.4359   0.4359   0.4615   0.3846   0.3846
D._pilosanthera_    | 0.1795   0.2821   0.2821   0.2821   0.3077   0.3333
D._pilosanthera_    | 0.2308   0.2821   0.2821   0.2821   0.3077   0.3333
D._pilosanthera_    | 0.2308   0.2821   0.2821   0.2821   0.3077   0.3333

                     D._blanc D._blanc D._blanc D._celeb D._celeb D._cauli
                    ------------------------------------------------------------
D._blancoi_3        | 1.0000
D._blancoi_4        | 0.7692   1.0000
D._blancoi_5        | 0.8205   0.9231   1.0000
D._celebica_1       | 0.7692   0.6923   0.6923   1.0000
D._celebica_2       | 0.8205   0.7179   0.7692   0.8462   1.0000
```

```
D._cauliflora_1     | 0.4103   0.3333   0.3333   0.4615   0.3846   1.0000
D._cauliflora_2     | 0.4103   0.3333   0.3333   0.4615   0.3846   1.0000
D._pilosanthera_    | 0.3590   0.3077   0.3333   0.3846   0.3846   0.4359
D._pilosanthera_    | 0.3590   0.3590   0.3846   0.3846   0.4359   0.4359
D._pilosanthera_    | 0.3590   0.3590   0.3846   0.3846   0.4359   0.4359

                          D._cauli D._pilos D._pilos D._pilos
                    -------------------------------------------------------------------------
D._cauliflora_2     | 1.0000
D._pilosanthera_    | 0.4359   1.0000
D._pilosanthera_    | 0.4359   0.8974   1.0000
D._pilosanthera_    | 0.4359   0.8974   1.0000   1.0000
```