Journal of Tropical Forest Science 25(3): 361–374 (2013)

PHENOLOGY IN FUNCTIONAL GROUPS OF CENTRAL AFRICAN RAINFOREST TREES

C Couralet[1, 2, *], J Van den Bulcke[2], LM Ngoma[3], J Van Acker[2] & H Beeckman[1]

[1]*Laboratory of Wood Biology and Xylarium, Royal Museum for Central Africa, Tervuren, Belgium*
[2]*Laboratory of Wood Technology, Department of Forest and Water Management, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium*
[3]*Institut National pour l'Etude et la Recherche Agronomiques, Luki, Democratic Republic of Congo*

Received May 2012

COURALET C, VAN DEN BULCKE J, NGOMA LM, VAN ACKER J & BEECKMAN H. 2013. Phenology in functional groups of Central African rainforest trees. A good understanding of the phenology of rainforest trees would help in anticipating ecosystem response to future global climate change. Extensive and long-term phenological observations in the tropics are rare and difficult to realise but unpublished historical records have been preserved and are of high value. Phenological data gathered between 1948 and 1957 on 3642 trees of 158 species in the rainforest reserve of Luki, Democratic Republic of Congo were analysed. Patterns of leaf shedding, flowering, fruiting and fruit dispersal were presented for three major functional groups of trees and their relationships with rainfall investigated. Annual rhythms of leaf and reproductive phenology were observed with patterns ranging from synchronous annual peaks to continuity. Over the years, positive association was found between leaf shedding and annual rainfall for shade-tolerant canopy species as well as between reproductive phenology and annual rainfall for long-lived heliophilous and shade-tolerant understorey species. Direct and indirect associations with intra-annual and supra-annual climate variations suggest that changes in environmental conditions may affect phenological patterns of tropical trees thus species interactions and ecosystem dynamics. The different leaf and reproductive phenological patterns found in different functional groups of trees promote the coexistence of numerous tree species in tropical rainforest multispecies communities. The associations between tree phenology and rainfall also reinforce the evidence for potential effects of climate variations on the ecology of Central African forests.

Keywords: Democratic Republic of Congo, climate change, phenological rhythms, plant–climate interactions, tropical rainforest

COURALET C, VAN DEN BULCKE J, NGOMA LM, VAN ACKER J & BEECKMAN H. 2013. Fenologi kumpulan berfungsi pokok hutan hujan di Afrika Tengah. Pemahaman baik tentang fenologi pokok hutan hujan dapat membantu kita menjangka gerak balas ekosistem terhadap perubahan iklim global masa hadapan. Pemerhatian fenologi jangka panjang dan meluas di kawasan tropika jarang dan sukar dilaksanakan tetapi rekod sejarah yang tidak diterbitkan adalah terpelihara dan rekod ini amat bernilai. Data fenologi yang dikumpul antara tahun 1948 hingga tahun 1957 melibatkan 3642 batang pokok daripada 158 spesies di Hutan Hujan Simpan Luki di Republik Demokratik Congo dianalisis. Corak luruhan daun, pembungaan, penghasilan buah dan penyebaran buah dilaporkan bagi tiga kumpulan berfungsi pokok yang utama dan perhubungan antara kumpulan ini dengan hujan dikaji. Pola tahunan fenologi daun dan fenologi pembiakan berubah dari puncak tahunan yang berlaku serentak kepada keadaan berterusan. Selepas beberapa tahun, perhubungan positif dicerap antara luruhan daun dengan hujan tahunan bagi spesies kanopi tahan naung. Fenologi pembiakan spesies heliofilus usia panjang dan spesies tingkat bawah tahan naung juga menunjukkan hubungan positif. Perhubungan secara langsung dan tidak langsung dengan variasi iklim dalam tahun dan luar tahun mencadangkan yang perubahan keadaan alam sekitar mungkin mempengaruhi corak fenologi pokok tropika dan seterusnya interaksi spesies serta dinamik ekosistem. Corak fenologi daun dan fenologi pembiakan yang berlainan yang terdapat dalam kumpulan berfungsi berlainan menggalakkan kewujudan bersama pelbagai spesies pokok dalam komuniti pelbagai spesies di hutan hujan tropika. Perhubungan antara fenologi pokok dengan hujan juga memperkukuh bukti bagi potensi kesan variasi iklim terhadap ekologi hutan di Afrika Tengah.

INTRODUCTION

Plant phenology is the study of recurring life-cycle events including leaf formation and fall, flowering, fruiting and seed dispersal (Morisette et al. 2009). Phenological events are controlled

---

*couraletc@yahoo.fr

by a combination of abiotic and biotic factors that determine their occurrence or inhibition (van Schaik et al. 1993). Phenology has been studied mostly in the temperate zone where patterns comply with regular climate seasonality (Menzel et al. 2005). In winter, low temperatures and short photoperiods limit cambial activity and cause dormancy in most plants. Then in spring reproductive and leaf cycles resume when temperature and photoperiod rise again. In the tropics, although plants can also cue their activities to temperature and photoperiod, water availability is the main driving force of phenological patterns (Singh & Kushwaha 2005). Consequently, weakly seasonal tropical climates or climates with low water stress during the dry season induce high phenological plasticity and great diversity of phenological strategies (Borchert 1999). Almost every possible phenological behaviour has been observed in tropical rainforests, from nearly continuous activity to repeated brief bursts and from complete intraspecific synchrony to complete asynchrony (Singh & Kushwaha 2006).

However, seasonal patterns of phenological activity are common in tropical rainforests (Boulter et al. 2006, Stevenson et al. 2008). Leaf abscission in the tropics is synchronised with dry conditions related to soil water content and tree water status (Borchert 1994). Leaf fall usually occurs during or at the end of the dry season and flushing in the wet season. Leaf fall and flushing can also be continuous for certain groups of species or at sites where moisture stress is never marked, resulting in the trees never being completely leafless (Singh & Kushwaha 2006). The amount of deciduousness can vary depending on the forest layer. Trees of the upper canopy have a tendency to be more deciduous and seasonal than the lower storeys (Bradley et al. 2011). Distinct seasonal flushing of leaves and small but significant seasonality in leaf abscission and leaf flushing are shown in the canopy of central Amazonian forests (Haugaasen & Peres 2005). However, in a Costa Rican wet tropical forest, shade-tolerant canopy species are mostly evergreen (O'Brien et al. 2008). With regard to reproductive phenology, flowering peaks have mostly been observed at the end of the dry season or at the onset of the rainy season (Stevenson et al. 2008), but canopy trees tend to flower during drier periods (van Schaik et al. 1993). The timing of fruiting often coincides with the start of the rainy season (Morellato et al. 2000), but patterns of fruit production are highly variable. Fruiting can peak at the end of the wet season and the start of the dry season or be extended throughout the entire dry season. Pioneer species usually produce fruits every year and have extended fruiting periods, while shade-tolerant canopy species generally have irregular fruiting periods and can experience mast fruiting (Muhanguzi & Ipulet 2012). In addition, multiannual scale changes in flower and fruit abundance usually conform to rainfall fluctuations for both understorey and canopy species (Bullock & Solis-Magallanes 1990).

Recent years have seen an increased interest in plant phenology because it may be an important mechanism behind ecosystem response to future global climate change (Morisette et al. 2009, Körner & Basler 2010). The Congo Basin is the second largest continuous area of rainforest in the world but only a few long-term studies of tree phenology have been reported in the region (Anderson et al. 2005, Chapman et al. 2005, Yamagiwa et al. 2008, Muhanguzi & Ipulet 2012). The existence of old long-term phenological records in the Democratic Republic of Congo (DRC) enables us to complement this knowledge. In 1948 a large-scale phenological survey was conducted at the rainforest reserve of Luki at the extreme west of the DRC. For 10 years, 3750 trees of more than 150 species were monitored on a 10-day basis for leaf fall, flowering, fruiting and dispersal of fruits. The extensive dataset allows for description of temporal phenological patterns in the community of trees of a tropical rainforest and their changes in relation to rainfall. Future climate is expected to be globally warmer and drier in tropical Africa (Bonan 2008, Koenig 2008). Phenological records (1948–1957) showed that annual rainfall was significantly lower between 1951 and 1954, with a severe drop in 1953–1954, most likely due to the drying effect of El Niño. Then rainfall levels returned to normal in the last years of monitoring. These historical variations in rainfall enable observation of phenological responses of trees to drier conditions anticipated in the region.

In this research, we studied the phenology of tropical trees in functional groups of species. Functional groups are a collection of species with similar impacts on their ecosystem, demographics and responses to perturbations (Condit et al. 1996). The grouping of species contains a fair amount of subjectivity and ideally it would be preferable to consider species individually. However, in systems with high species diversity, analyses at the species level would mean a low number of individuals per species, thus no possibility of generalisation (Gourlet-Fleury et al. 2005). The allocation of several species to a small number of groups increases the size of the sample used to exhibit patterns. Using functional groups instead of species also allows comparisons with other similar forests and the formulation of general hypotheses based on the results.

In the present study, we described temporal variations of leaf, flower and fruit phenology in functional groups of tree species in a tropical rainforest of the Congo Basin. We also examined how these phenological patterns varied in relation to changes in rainfall and made comparison with other tropical sites.

Despite seasonal rainfall in Luki, humidity is high (> 80%) throughout the year. This raises several obvious questions that are the central focus of this study: (1) does foliar and reproductive phenology of rainforest trees at Luki exhibit temporal patterning associated with seasonality in precipitation? (2) are these patterns consistent or comparable with observed phenological patterns in other tropical forests with varying degrees of rainfall seasonality? and (3) under predicted future climate scenarios in which rainfall over tropical Africa decreases, what are the expected phenological consequences for tropical rainforest trees in the region?

MATERIALS AND METHODS

Study site

The Luki Forest Reserve is located in south-western DRC, 30 km north from the port city of Boma. It is the southernmost remnant of the highly diverse Mayombe forest and lies in a hilly landscape with an altitude of 150 to 500 m above sea level (Monteiro 1962). The sloppy terrain favours heavy erosion and prevents the formation of deep soils (Monimeau 1990). The soil is very heterogeneous but has been described as generally ferrallitic, acid and with poor chemical content. Climatic data are available from the Luki meteorological station (5° 38' N, 13° 7' E) from 1947 till present. Average annual temperature and rainfall estimates are 24.6 °C and 1180 mm respectively. Rainfall is seasonal with a major dry period of less than 60 mm of monthly precipitation from June till September (Couralet et al. 2010). However, the hilly landscape and the vicinity of the Atlantic Ocean cause frequent mist and dense cloud cover that maintain relative air humidity above 80% (Pendje & Baya ki 1992, Lubini 1997, Couralet et al. 2010). Contrary to what is usually observed in monsoonal climates (Malhi et al. 2002), air temperature and solar irradiance are also positively correlated with rainfall ($r = 0.64$, $p < 0.001$, 1948–2006 and $r = 0.85$, $p < 0.001$, 1959–1994 respectively). Consequently, despite relatively low annual rainfall and three to four months with less than 60 mm of precipitation per year, plants do not suffer extreme water stress during the dry season. The result is a weak seasonal tropical climate, which has allowed a tropical semi-evergreen rainforest of the Guineo-Congolian domain to establish in Luki (Lubini 1997, Whitmore 1998).

Data and analyses

At the Luki Forest Reserve, 3750 woody plants were monitored every 10 days from January 1948 till December 1957 for leaf shedding, flowering, fruiting and dispersal of fruits. Methodological details, i.e. how the phenological stages were determined or how observations of crowns were made were not available. The species composition of the sample (proportions of individuals per species) was very similar to the species composition of the same forest today (Couralet 2011), which indicates that the selection of trees for monitoring must have been done randomly. The data were scored as present/absent and were originally handwritten on notebooks conserved in the herbarium of Luki. They were digitised and converted to Excel. Species were initially referred to by vernacular names (Kiyombe language) and the corresponding scientific names were found with the help of African florae (Hutchinson 1927–1936, INEAC 1948–1960, Aubréville 1961). Among the individual stems, 15 were lianas and 93 remained in the category 'unknown' either because they were unidentified at the time of monitoring or because their given vernacular name could not be associated with a present scientific name. These records were excluded from analyses. Eventually, phenological data of 3642 trees from 158 species were used in this study (Appendix).

Species were grouped according to their main functional traits and timing of their dominance in forest succession (Hawthorne 1995, Chazdon et al. 2010). The maximum potential tree size was also considered, indicating in which forest layer (understorey or canopy) a species was mostly found at maturity. This approach resulted in three major functional groups (short-lived pioneers were not considered in the 1948 survey): (1) group CAN: long-lived shade-tolerant species that dominated the forest canopy at maturity (e.g. the most abundant species (192 trees) was *Prioria balsamifera*), (2) group HEL: long-lived heliophilous or semi-heliophilous species mostly found in the canopy at maturity (corresponding to the non-pioneer light-demanding guild of hawthorne; e.g. the most abundant species (184 trees) was *Terminalia superba*) and (3) group UND, long-lived, shade-tolerant and generally small-statured species that occupied the understorey at maturity (e.g. the most abundant species (120 trees) was *Xylopia wilwerthii*).

For each species, the proportion of trees for which a phenological event was observed was calculated for every 10-day period using MATLAB®. Average time series were plotted over 10 years of monitoring for the three functional groups. To highlight seasonal tendencies, the proportions of trees were averaged for the whole period into monthly values represented on annual bar graphs.

To verify whether species belonging to each functional group had similar phenological behaviour, a clustering analysis was performed based on the time series of all phenological events for the five most abundant species of each group (abundance ranging from 31 to 147 trees per species, median = 88 trees).

A similar clustering procedure as described by Basalto et al. (2007) was implemented in MATLAB®. The similarity metric function d_{ij} was based on the Pearson's correlation coefficients c_{ijp} between the profiles of each phenological event of all trees.

$$d_{ij} = \sqrt{2\left(4 - \sum_{p=1}^{4} c_{ijp}\right)}$$

where p = phenological events and i and j = two different tree species.

This metric was used as input for Ward's linkage to form the cluster tree. Other linkage algorithms were tried as well and no differences were found for this specific clustering case.

The phenological data were also compared with variations in rainfall. Rainfall records were available from the Luki meteorological station for the whole monitoring period but air temperature was available only for the last year (1957). For the three functional groups of species, Pearson correlations were calculated between the maximum proportions of trees showing leaf shedding, flowering, fruiting and dispersal of fruits and the annual sum of precipitation for the same period (1948–1957).

RESULTS

General tendencies in phenological activity during the 10 years of monitoring

In all functional groups, the synchronicity of all phenological events was generally very low. For example, the maximum percentage of trees shedding leaves simultaneously was 19% (CAN group in 1949) with an average maximum of only 8% (Figure 1). The maximum percentage of trees flowering simultaneously was 55% (HEL group in 1951) with an average maximum of 22%. Various patterns of leaf shedding, flowering, fruiting and dispersal of fruits were observed, from sharp peaks to continuity but always with annual periodicity. The time series of phenological events also revealed annual periodicity in leaf shedding, flowering, fruiting and dispersal of fruits for all groups of species, although most clearly for the heliophilous species (Figure 1). A general decrease in the proportion of observed phenological events occurred for all groups from 1951, reaching a minimum in 1954 then regaining previous levels in 1957.

The dendrogram resulting from the cluster analysis exhibited three distinct groups (Figure 2). The upper one composed mainly of understorey species and the lower one, heliophilous species. Shade-tolerant canopy species were found in the three groups and the middle group contained members of all three functional groups.

Leaf phenology

In the three functional groups, leaf shedding started during the dry period (July–August) and was maximum at the transition between the dry and rainy seasons (September–October) (Figures 1 and 3). The shade-tolerant canopy species had

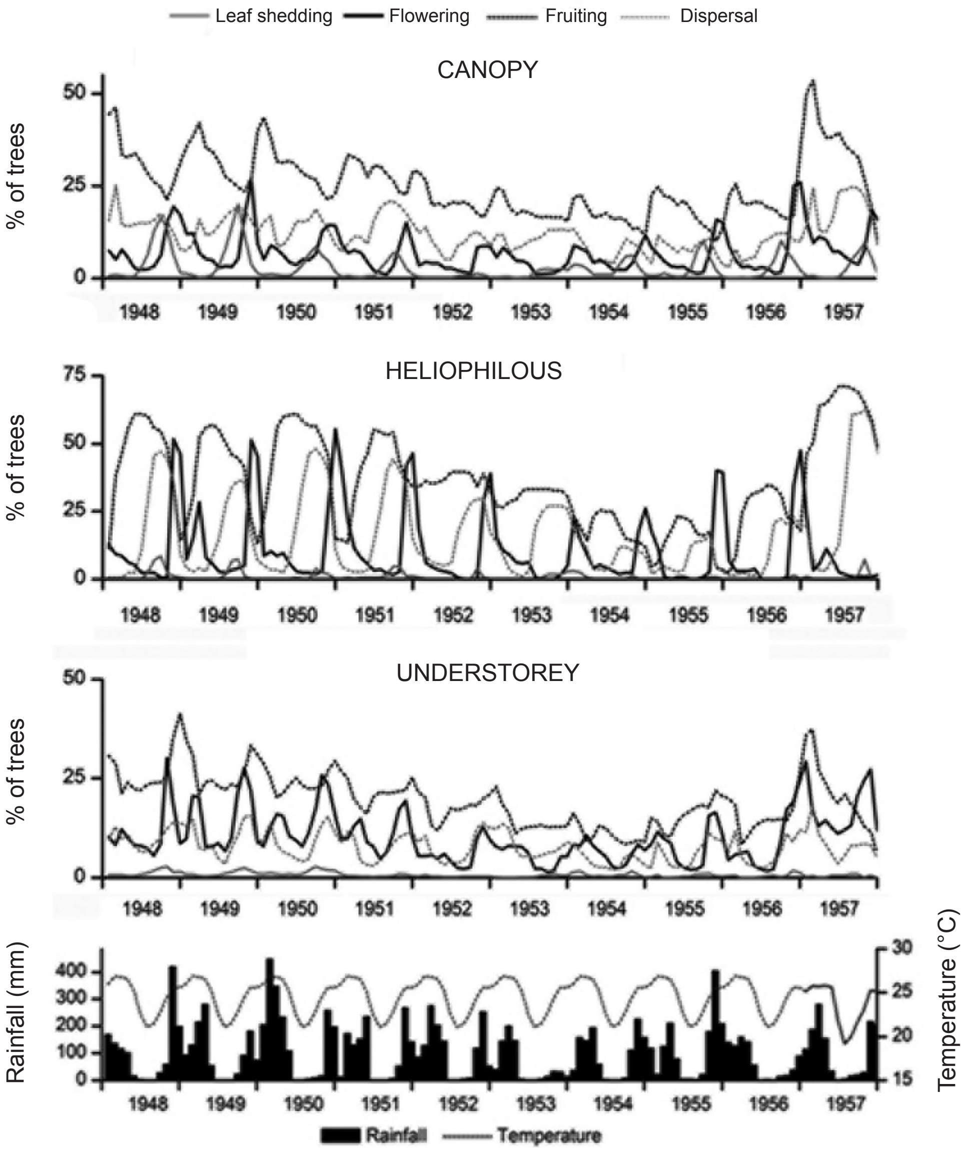

Figure 1 Monthly time series of reproductive and leaf phenology for three functional groups of trees and records of rainfall and temperature for the period 1948–1957 in the forest reserve of Luki

the clearest pattern of leaf shedding with up to 20% of trees shedding leaves in September, while only a small proportion (2%) of understorey trees shed leaves simultaneously (Figure 3). In heliophilous species, leaf shedding was also maximum during the transition between dry and rainy seasons but for a very limited number of trees (5%).

Reproductive phenology (flowering, fruiting and dispersal of fruits)

Overall, the different reproductive stages were observed in all periods of the year (Figures 1 and 3). The heliophilous group had the clearest periodicity of reproductive stages (Figure 1). Sharp flowering peaks were observed just after the shedding of leaves in a short period around November which was the beginning of the rainy season. A second peak of flowering was also observed at the end of the rainy season (March–April), as evident in 1948 and 1957. Fruiting and dispersal of fruits followed flowering with a lag of approximately 5 and 10 months respectively. Both events were spread out over time. For canopy and understorey species, flowering was also maximum from September till October but the proportions of trees were much smaller and peaks were less sharp compared with the heliophilous group (Figures 1 and 3). Maximum production and dispersal of fruits occurred early after flowering peaks (after 1 or 2 months),

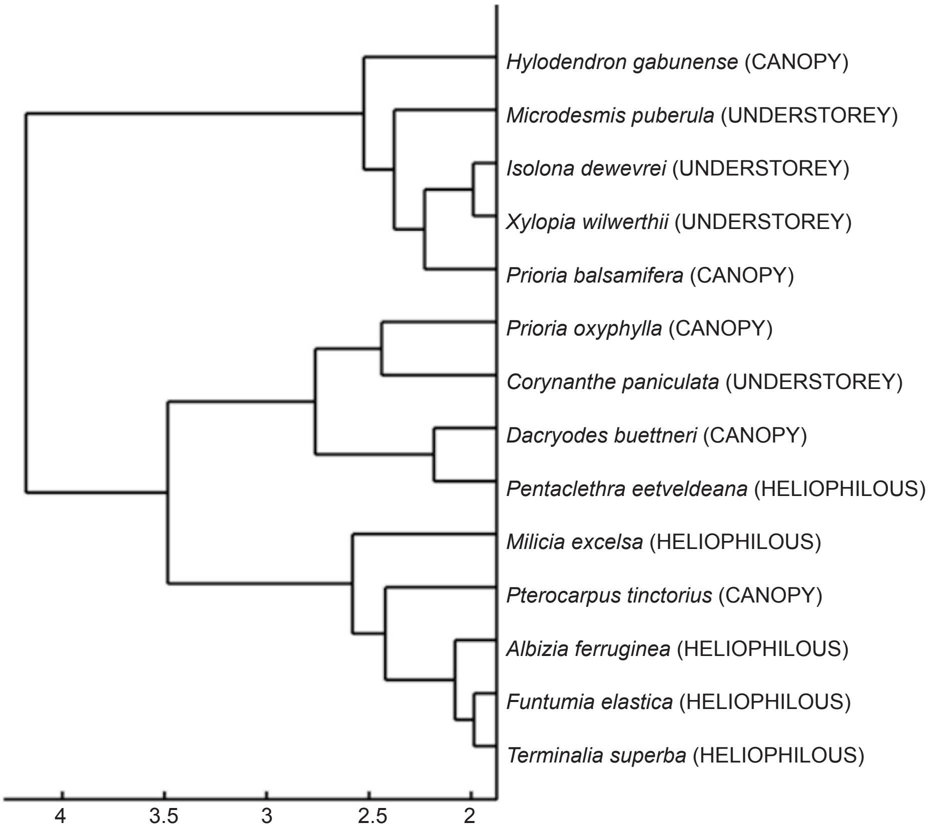

Figure 2 Clustering based on the time series of phenological events for the most abundant species of each functional group using standard linkage algorithms

unlike those for light-demanding species (after 5 months).

Phenology in relation to rainfall

Flowering generally started at the beginning of the rainy season (Figures 1 and 3). For understorey species, two flowering peaks were observed—the first at the beginning of the rainy season (September–October) and the second at the restart of rains after the minor dry season (March).

High positive correlation (0.85) was found between the maximum proportion of trees shedding leaves and total annual rainfall for canopy species (Table 1). Significant positive correlations between flowering and rainfall were found for heliophilous (0.67) and understorey species (0.68) ($p < 0.05$).

DISCUSSION

The conventional grouping of species according to their light preference and position in the canopy at the adult stage was supported by the grouping of species according to their phenology. However, the distinction was clear for the shade-tolerant understorey and long-lived heliophilous species only. This can be explained by strong differences between the two functional groups of species in terms of growth environment (e.g. low vs high light levels) and life history (e.g. slow vs fast growth) which may also affect their phenological strategies. On the other hand, canopy species are mostly defined by the dominance of trees in their adult stage, which can be the result of various life histories and phenological strategies. Clustering was performed based on all phenological events so it was difficult to tell the phenological pattern of the species. This calls for additional analysis at the species level.

The 10-year phenological monitoring of trees at Luki revealed annual rhythms of leaf and reproductive cycles for the three functional groups of species. Although peaks were distinct, the proportion of trees being simultaneously in the same phenological stage rarely exceeded 50%. Each phenological stage could be observed at any time of the year. This is commonly seen in

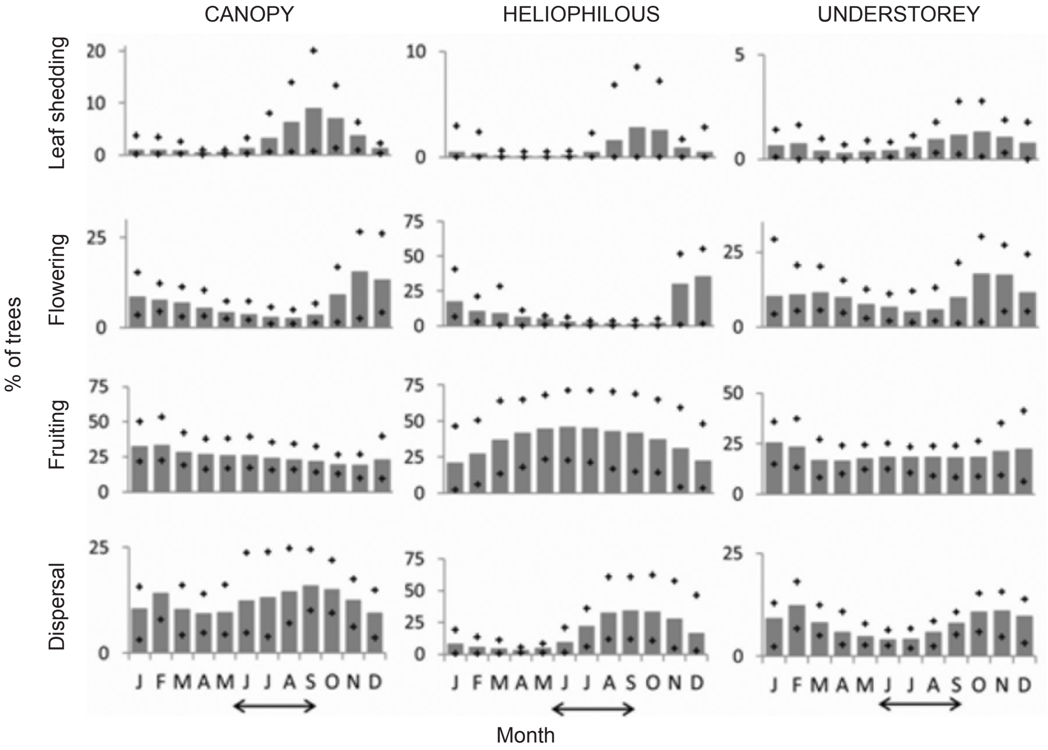

Figure 3 Phenological seasonality for the three functional groups of trees in the reserve of Luki; bars represent average percentages and crosses indicate maximum and minimum values from 1948–1957; black arrows indicate the dry season

Table 1 Pearson correlations between the maximum proportion of trees in which leaf shedding, flowering, fruiting and dispersal of fruits were observed and the annual sum of rainfall ($p < 0.05$) for the three functional groups

Group	Leaf shedding	Flowering	Fruiting	Dispersal
Canopy	0.85	0.47	0.12	-0.20
Heliophilous	-0.21	0.67	-0.17	-0.27
Understorey	-0.04	0.68	0.20	0.37

tropical forests, even with highly seasonal tropical climates (Williams et al. 1999). Flowering and fruiting require hydrated stems and these are facilitated by deep root systems or trunk water storage (Schöngart et al. 2002). At Luki, the local atmospheric conditions maintain a high level of air humidity all year round. This probably allows leaf shedding, flowering and fruiting to occur at any time of the year in most tree species (Morellato et al. 2000).

Leaf phenology

For all groups of species, common periods of leaf shedding with annual frequencies were observed, reaching maximum in September–October, thus at the transition between the dry and rainy seasons. The proportions of trees simultaneously shedding leaves were, however, very low for all functional groups. In fact, no tree species could be classified as deciduous, semi-deciduous or brevi-deciduous according to existing phenological classifications (Kushwaha & Singh 2005). This suggests that many of these species may be 'leaf exchangers', shedding leaves and almost simultaneously growing a new set (Singh & Kushwaha 2006). In many species, leaf shedding also has a triggering role for flowering, as a result of stem rehydration at the onset of the wet season.

For understorey and long-lived heliophilous species, no significant relationship was found between levels of leaf shedding and monthly rainfall. On the other hand, levels of leaf shedding for canopy species correlated positively with total annual rainfall. The effect of variations in air and soil humidity or water availability is usually weaker for trees growing under dense vegetation cover than for taller trees directly exposed to climatic variations (Lowman & Wittman 1996). Rainfall-induced leaf abscission was previously observed but rare (Elliott et al. 2006, Mehltreter & Garcia-Franco 2009). Higher leaf shedding during wet years could be due to lack of irradiance or waterlogged soils as a result of the specific climatic conditions (thick cloud cover during the dry season and constantly high air humidity). The constantly high levels of air humidity in Luki may also explain that trees generally do not suffer from water deficit. Leaf shedding may only be partial for most trees, even for species that are usually strictly deciduous but have intermediary habits in such climatic conditions. Such phenological plasticity has been shown in temperate trees growing in tropical climates (Borchert et al. 2005) and tropical species with large distribution ranges (Borchert et al. 2004).

Reproductive phenology

Annual patterns of reproductive phenology were observed in functional groups of species in Luki between 1948 and 1957. In all functional groups, flowering mostly occurred immediately after leaf shedding, at the onset of the rainy season. A second peak of flowering was also often observed at the end of the rainy season, especially for understorey trees. The first flowering peak can be explained by the influence of the first rains after the dry season on bud break. In seasonal tropical climates, flowering is often triggered by the first rains of the rainy season (sometimes via leaf shedding) and is thus concentrated in the transition from the late dry to the early wet season (Stevenson et al. 2008). However, flower production has also been reported to coincide with peaks of irradiance (Wright & van Schaik 1994). At Luki the dry season is cloudy and solar irradiance gets higher during the rainy season with a maximum in March, which can explain the second peak of flowering (Couralet et al. 2010). Subsequent fruit formation mostly occurred during the second half of the rainy season as observed in other studies (Selwyn & Parthasarathy 2007). Fruiting was, however, observed all year long for the heliophilous and understorey groups and maximum dispersal of fruits occurred mostly before the end of the rainy season. These results support the hypothesis that adequate development time from flowering to fruit dispersal has been achieved so that seeds are released in rainy periods when germination is most likely to be induced and seedlings start growing with low probability of drought (Stevenson et al. 2008). Although other abiotic factors may be involved, these results confirm the direct or indirect role of rainfall on the promotion of bud break and subsequent flowering in tropical trees (Fenner 1998). While regular annual periodicity was found for maximum frequencies of flowering and fruiting, patterns varied widely among species as commonly seen in tropical forests (Newstrom et al. 1994).

The heliophilous group showed sharp flowering peaks followed by fruiting over several months. However, in the understorey and canopy groups, reproductive patterns appeared erratic. Each pattern can be seen as a response to a different set of selective pressures. Strong peaks of flowering and fruiting are common for deciduous species and for species that are pollinated and dispersed by animals, suggesting disadvantages to out-of-season individuals (Stevenson et al. 2008). Moreover, fruiting peaks at the community level may be favoured because they avoid the pressure of seed predators through satiation effect (van Schaik et al. 1993). On the other hand, irregular patterns may be due to inconsistent selective pressures such as year-to-year variations in environmental conditions or changes in pollinator or predator abundances (Fenner 1998). Levels of reproductive events (flowering, fruiting and dispersal of fruits) were globally high in 1948, 1949 and 1950 but steadily decreased between 1951 and 1955. Frequencies were especially low in 1954 for all trees, which might be explained by the very low rainfall in 1953–1954 caused by an El Niño event. Annual sums of precipitations were slightly above average in 1948 and 1949 (1268 and 1260 mm respectively compared with 1180 mm on average for the period 1948–2006) and remarkably high in 1950 (1845 mm). The reproductive processes observed during those years may thus have been above their usual levels. On the other hand, the annual sum of precipitation was only 654 mm in 1953, which was the driest year of the period 1948–2006. Until 1955, the sum of rainy season precipitations remained below average, with monthly rainfall never above 300 mm. Trees may thus have suffered water deficit, resulting in weakened and/or delayed reproductive activity. The tendency was most marked for light-demanding species usually growing in open spaces and consequently more prone to experience temporary droughts. Moreover, mast fruiting years were observed for all groups of species in 1956–1957 when rainfall regained high levels after a 4-year drier period. Positive correlations between the frequencies of reproductive events and rainfall also support the view that the reproductive activity of tropical rainforest trees is globally associated with rainfall levels through changes in tree water status (Singh & Kushwaha 2005).

Despite a weakly seasonal climate, the leaf and reproductive phenology of trees in the rainforest of Luki was associated with seasonal variations in rainfall between 1948 and 1957. Phenological variations were also correlated with year-to-year changes in precipitation. In particular, low levels of flowering and fruiting were observed during dry years caused by an El Niño episode. This does not demonstrate that rainfall is the proximate cue regulating phenology. Multiple climatic factors are likely to covary and several other biotic or abiotic factors may be at play (Forrest & Miller-Rushing 2010). Investigations on temperature and day length would help us better understand the influence of climatic variations on phenology. However, based on our results the expected climate changes in tropical Africa are potential driving forces for important phenological changes and, in turn, major vegetation changes.

ACKNOWLEDGEMENTS

We thank the Institut National pour l'Etude et la Recherche Agronomiques, Man And Biosphere programme and World Wide Fund (DRC and Belgium) for support. We are grateful particularly to L Nsenga, JBN Loli, S Mutambue, B Toirambe, M Tsimbal, JMM Songo and FM Phaka for assistance and to I Heinrich for advice and discussion. The postdoctoral funding for J Van den Bulcke was granted by the Research Foundation—Flanders (FWO-Belgium).

REFERENCES

Anderson D, Nordheim E, Moermond T, Zoro & Boesch C. 2005. Factors influencing tree phenology in Tai National Park, Cote d'Ivoire. *Biotropica* 37: 631–640.

Aubréville A. 1961. *Flore du Gabon*. Museum National d'Histoire Naturelle, Paris.

Basalto N, Bellotti R, De Carlo F, Facchi P, Pantaleo E & Pascazio S. 2007. Hausdorff clustering of financial time series. *Physica A: Statistical Mechanics and its Applications* 379: 635–644.

Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.

Borchert R. 1994. Water status and development of tropical trees during seasonal drought. *Trees—Structure and Function* 8: 115–125.

Borchert R. 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. *IAWA Journal* 20: 239–247.

Borchert R, Meyer SA, Felger RS & Porter-Bolland L. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13: 409–425.

Borchert R, Robertson KS, Schwartz MD & Williams-Linera G. 2005. Phenology of temperate trees in tropical climates. *International Journal of Biometeorology* 50: 57–65.

Boulter SL, Kitching RL & Howlett BG. 2006. Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology* 94: 369–382.

Bradley AV, Gerard FF, Barbier N, Weedon GP, Anderson LO, Huntingford C, AragÃO LEOC, Zelazowski P & Arai E. 2011. Relationships between phenology, radiation and precipitation in the Amazon region. *Global Change Biology* 17: 2245–2260.

Bullock SH & Solis-Magallanes JA. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22: 22–35.

Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ & Poulsen JR. 2005. A long-term evaluation of fruiting phenology: importance of climate change. *Journal of Tropical Ecology* 21: 31–45.

Chazdon R, Finegan B, Capers RS, Salgado-Negret B, Casanoves F, Boukili V & Norden N. 2010. Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. *Biotropica* 42: 31–40.

Condit R, Hubbell SP & Foster RB. 1996. Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* 7: 405–416.

Couralet C. 2011. Community dynamics, phenology and growth of tropical trees in the rain forest reserve of Luki, Democratic Republic of Congo. PhD thesis, Ghent University, Ghent.

Couralet C, Sterck FJ, Sass-Klaassen U, Van Acker J & Beeckman H. 2010. Species-specific growth responses to climate variations in understory trees of a Central African rain forest. *Biotropica* 42: 503–511.

Elliott S, Baker PJ & Borchert R. 2006. Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and Biogeography* 15: 248–257.

Fenner M. 1998. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 78–91.

Forrest J & Miller-Rushing AJ. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3101–3112.

Gourlet-Fleury S, Blanc L, Picard N, Sist P, Dick J, Nasi R, Swaine MD & Forni E. 2005. Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. *Annals of Forest Science* 62: 785–796.

Haugaasen T & Peres CA. 2005. Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica* 37: 620–630.

Hawthorne WD. 1995. *Ecological Profiles of Ghanaian Forest Trees.* Oxford Forestry Institute, Oxford.

Hutchinson J. 1927–1936. *The Flora of West Tropical Africa.* Crown Agents for Oversea Governments and Administrations –Royal Botanic Gardens, London.

INEAC. 1948–1960. *Flore du Congo belge et du Ruanda-Urundi.* Institut National pour l'Etude Agronomique du Congo Belge, Brussels.

Koenig R. 2008. Critical time for African rainforests. *Science* 320: 1439–1441.

Körner C & Basler D. 2010. Phenology under global warming. *Science* 327: 1461–1462.

Kushwaha CP & Singh KP. 2005. Diversity of leaf phenology in a tropical deciduous forest in India. *Journal of Tropical Ecology* 21: 47–56.

Lowman MD & Wittman PK. 1996. Forest canopies: methods, hypotheses, and future directions. *Annual Review of Ecology and Systematics* 27: 55–81.

Lubini CA. 1997. *La végétation de la Réserve de Biosphère de Luki au Mayombe (Zaïre).* Opera Botanica Belgica, Meise.

Malhi Y, Pegoraro E, Nobre AD, Pereira MGP, Grace J, Culf AD & Clement R. 2002. Energy and water dynamics of a central Amazonian rain forest. *Journal Geophysical Research* 107.

Mehltreter K & Garcia-Franco JG. 2009. Leaf phenology and trunk growth of the deciduous tree fern *Alsophila firma* (Baker) D.S. Conant in a lower montane Mexican forest. *American Fern Journal* 98: 1–13.

Menzel A, Estrella N & Testka A. 2005. Temperature response rates from long-term phenological records. *Climate Research* 30: 21–28.

Monimeau A. 1990. *Etude des Solutions du sol sous Forêt Dense Équatoriale. Bilan d'un an de collecte à Dimonika (Mayombe, Congo), Mars 1989–Mars 1990.* ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération), Pointe-Noire.

Monteiro RFR. 1962. Le massif forestier du Mayumbe angolais. *Bois et Forêts des Tropiques* 82: 3–17.

Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC & Zipparro VB. 2000. Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* 32: 811–823.

Morisette JT, Richardson AD, Knapp AK, Fisher JI, Graham EA, Abatzoglou J, Wilson BE, Breshears DD, Henebry GM, Hanes JM & Liang L. 2009. Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment* 7: 253–260.

Muhanguzi HDR & Ipulet P. 2012. Fruiting phenology of fig trees in Kalinzu Forest, Uganda. *African Journal of Ecology* 50: 90–101.

Newstrom LE, Frankie GW & Baker HG. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain-forest trees at La-Selva, Costa-Rica. *Biotropica* 26: 141–159.

O'Brien J, Oberbauer SF, Clark DB & Clark DA. 2008. Phenology and stem diameter increment seasonality in a Costa Rican wet tropical forest. *Biotropica* 40: 151–159.

Pendje G & Baya ki M. 1992. La *Réserve de Biosphère de Luki (Mayombe, Zaïre). Patrimoine Floristique et Faunistique en Péril.* PNUD-UNESCO-MAB, Paris.

van Schaik CP, Terborgh JW & Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353–377.

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V & Worbes M. 2002. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology* 18: 581–597.

Selwyn MA & Parthasarathy N. 2007. Fruiting phenology in a tropical dry evergreen forest on the Coromandel coast of India in relation to plant life-forms, physiognomic groups, dispersal modes, and climatic constraints. *Flora —Morphology, Distribution, Functional Ecology of Plants* 202: 371–382.

Singh KP & Kushwaha CP. 2005. Emerging paradigms of tree phenology in dry tropics. *Current Science* 89: 964–975.

Singh KP & Kushwaha CP. 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Annals of Botany* 97: 265–276.

Stevenson PR, Castellanos MC, Cortés AI & Link A. 2008. Flowering patterns in a seasonal tropical lowland forest in western Amazonia. *Biotropica* 40: 559–567.

Whitmore TC. 1998. *An Introduction to Tropical Rain Forests.* Oxford University Press, Oxford.

Williams RJ, Myers BA, Eamus D & Duff GA. 1999. Reproductive phenology of woody species in a north Australian tropical savanna. *Biotropica* 31: 626–636.

Wright SJ & van Schaik CP. 1994. Light and the phenology of tropical trees. *American Naturalist* 143: 192–199.

Yamagiwa J, Basabose AK, Kaleme PK & Yumoto T. 2008. Phenology of fruits consumed by a sympatric population of gorillas and chimpanzees in Kahuzi Biega National Park, Democratic Republic of Congo. *African Study Monographs* (supplementary) 39: 3–22.

Appendix List of monitored species with their functional groups (CAN = canopy, HEL = heliophilous, UND = understorey)

Family/subfamily	Species	Vernacular name	Number of observed trees	Functional group
Fabaceae/Caesalpinioideae	*Afzelia bella*	Disukama	1	UND
Fabaceae/Caesalpinioideae	*Afzelia bipindensis*	–	6	CAN
Rubiaceae	*Aidia ochroleuca*	Tsania ya fioti	19	UND
Fabaceae/Mimosoideae	*Albizia ferruginea*	Kasa-kasa-di-nene	97	CAN
Fabaceae/Mimosoideae	*Albizia* sp.	Kasa kasa	7	CAN
Sapindaceae	*Allophyllus africanus*	Teba	11	CAN
Clusiaceae/Guttiferaceae	*Allanblackia floribunda*	Nionzo	29	CAN
Apocynaceae	*Alstonia congensis*	Tsonguti	1	CAN
Fabaceae/Faboideae	*Amphimas ferrugineus*	Tsala Kifutu	4	CAN
Annonaceae	*Annona senegalensis*	Nlolo tseke	5	UND
Fabaceae/Caesalpinioideae	*Anthonotha macrophylla*	Fussa	5	CAN
Anacardiaceae	*Antrocaryon nannanii*	Mungongo	35	CAN
Moraceae	*Antiaris toxicaria*	Tsangu	29	CAN
Sapotaceae	*Autranella congolensis*	Kungulu	4	CAN
Fabaceae/Caesalpinioideae	*Baikiaea insignis*	Posa mbuma	9	CAN
Passifloraceae	*Barteria dewevrei*	Munzinzi	13	CAN
Sapindaceae	*Blighia welwitschii*	Nguba	9	CAN
Rubiaceae	*Brenania brieyi*	Muandi	4	UND
Burseraceae	*Canarium schweinfurthii*	Bidikala	15	CAN
Meliaceae	*Carapa procera*	Nkazu nkumbi	34	UND
Bombacaceae	*Ceiba pentandra*	Mfuma	11	CAN
Ulmaceae	*Celtis mildbraedii*	Luniumbu	109	CAN
Ulmaceae	*Celtis* sp.	–	4	CAN
Sapotaceae	*Chrysophyllum africanum*	Lenge	14	CAN
Myristicaceae	*Coelocaryon botryoides*	Lomba nkumbi	25	CAN
Sterculiaceae	*Cola mahoundensis*	Madioni madioni	57	UND
Sterculiaceae	*Cola nitida*	Nkazu	2	UND
Sterculiaceae	*Cola* sp.	–	1	UND
Rubiaceae	*Corynanthe paniculata*	Tsania	117	UND
Fabaceae/Caesalpinioideae	*Cynometra lujae*	Cynometra	4	CAN
Burseraceae	*Dacryodes buettneri*	Safu Nkala	69	UND
Burseraceae	*Dacryodes edulis*	Safu	5	UND
Sapindaceae	*Deinbollia laurentii*	Disukama	21	UND
Fabaceae/Caesalpinioideae	*Dialium excelsum*	Vamu	13	CAN
Fabaceae/Caesalpinioideae	*Dialium pachyphyllum*	Tadi Nti	45	CAN
Fabaceae/Caesalpinioideae	*Dialium tessmannii*	Bekete	4	CAN
Euphorbiaceae	*Dichostemma glaucescens*	Mutsangi	2	CAN
Ebenaceae	*Diospyros heterotricha*	Pangi ya mundombe ndombe	1	UND

(continued)

Appendix (continued)

Ebenaceae	*Diospyros macrocarpa*	Tsembani	1	UND
Ebenaceae	*Diospyros* sp.	Mundombe Ndombe	16	UND
Euphorbiaceae	*Discoglypremna caloneura*	Dibimbi	18	CAN
Liliaceae	*Dracaena arborea*	Diba Di Nzambi	13	CAN
Annonaceae	*Enantia affinis*	Muamba mbuaki	9	UND
Meliaceae	*Entandrophragma angolense*	Mvovo	5	CAN
Meliaceae	*Entandrophragma utile*	Kalungi	4	CAN
Sapindaceae	*Eriocoelum microspermum*	Kote	41	CAN
Fabaceae/Faboideae	*Erythrina droogmansiana*	Disumba	5	UND
Fabaceae/Caesalpinioideae	*Erythrophleum suaveolens*	Nkasa	9	CAN
Moraceae	*Ficus exasperata*	Bubu Tsanda	1	CAN
Moraceae	*Ficus mucuso*	Kimbidi	5	CAN
Moraceae	*Ficus* sp.	Zingila	2	CAN
Moraceae	*Ficus variifolia*	Kaya	21	CAN
Fabaceae/Mimosoideae	*Fillaeopsis discophora*	Nsinga nsinga	2	CAN
Apocynaceae	*Funtumia elastica*	Bohumbanama	147	HEL
Sapindaceae	*Ganophyllum giganteum*	Nzembila	44	CAN
Clusiaceae	*Garcinia epunctata*	Bangu	11	UND
Meliaceae	*Guarea cedrata*	Ngongo	9	CAN
Clusiaceae	*Harungana madagascariensis*	Ntunu	7	HEL
Meliaceae	*Hexalobus crispiflorus*	Mbula Ndombe	28	CAN
Ulmaceae	*Holoptelea grandis*	Nemba	5	CAN
Huaceae	*Hua gabonii*	Mvenzi	9	UND
Fabaceae/Caesalpinioideae	*Hylodendron gabunense*	Pangu	99	CAN
Euphorbiaceae	*Hymenocardia ulmoides*	Mutseke Tseke	23	HEL
Irvingiaceae	*Irvingia gabonensis*	Mueba	3	CAN
Irvingiaceae	*Irvingia grandifolia*	Ntessie	15	CAN
Annonaceae	*Isolona dewevrei*	–	79	UND
Fabaceae/Caesalpinioideae	*Julbernardia arnoldiana*	Pangi Mbanda	12	CAN
Irvingiaceae	*Klainedoxa gabonensis*	Nkuma Nkuma	8	CAN
Anacardiaceae	*Lannea welwitschii*	Nkumbi	35	CAN
Meliaceae	*Lovoa trichilioides*	Voka Voka	10	CAN
Euphorbiaceae	*Macaranga monandra*	Nsasa	6	UND
Euphorbiaceae	*Macaranga spinosa*	Nsasa tsende	1	UND
Rhamnaceae	*Maesopsis eminii*	Mutsambi Tsambi	2	CAN
Euphorbiaceae	*Mallotus oppositifolius*	Ditamba Tamba	5	UND
Clusiaceae/Guttiferaceae	*Mammea africana*	Mboza	1	CAN
Sapotaceae	*Manilkara* sp.	Pangi Ya Lenge	12	UND
Euphorbiaceae	*Margaritaria discoidea*	Mvasa	1	CAN
Rosaceae	*Maranthes glabra*	Tadi Nti Parinari	8	UND
Bignoniaceae	*Markhamia tomentosa*	Ndawa	17	UND
Meliaceae	*Melia bambolo*	Mumfiba	1	UND
Euphorbiaceae	*Microdesmis puberula*	Tadi Tadi	45	UND

(continued)

Appendix (continued)

Fabaceae/Faboideae	*Millettia drastica*	Kodia Kodia	3	CAN
Moraceae	*Milicia excelsa*	Kambala	31	CAN
Fabaceae/Faboideae	*Millettia versicolor*	Lubota	17	HEL
Annonaceae	*Monodora angolensis*	Divinia monodora	37	CAN
Annonaceae	*Monodora myristica*	Mumbende Mbende	23	CAN
Rubiaceae	*Morinda lucida*	Nsiki	1	CAN
Cecropiaceae	*Musanga cecropioides*	Nsenga	10	HEL
Moraceae	*Myrianthus arboreus*	Mbuba	13	HEL
Rubiaceae	*Nauclea latifolia*	Ngulu maza ya tseke ntumbi	2	UND
Tiliaceae/Sterculioideae	*Nesogordonia leplaei*	Kondo finda kote	22	CAN
Fabaceae/Mimosoideae	*Newtonia leucocarpa*	Pangi nsinga	28	CAN
Sapotaceae	*Omphalocarpum sankuruense*	Nsakala	7	CAN
Flacourtiaceae	*Oncoba dentata*	–	2	UND
Flacourtiaceae	*Oncoba welwitschii*	Kwakwa	49	UND
Olacaceae	*Ongokea gore*	Nsanu	16	CAN
Passifloraceae	*Paropsia braunii*	Mumbiebie	17	UND
Fabaceae/Mimosoideae	*Parkia filicoidea*	Munzinzi	8	UND
Rubiaceae	*Pausinystalia macroceras*	Tsania welo	12	UND
Fabaceae/Mimosoideae	*Pentaclethra eetveldeana*	Tsamu	125	UND
Fabaceae/Mimosoideae	*Pentaclethra macrophylla*	Mvanza	50	CAN
Lecythidaceae	*Petersianthus macrocarpus*	Minzu	29	CAN
Fabaceae/Mimosoideae	*Piptadeniastrum africanum*	Nsinga	39	CAN
Papilionoideae	*Platysepalum chevalieri*	Nsala	6	UND
Sapindaceae	*Placodiscus resendeanus*	Muangula	14	UND
Annonaceae	*Polyalthia suaveolens*	Muamba Ndombe	42	UND
Fabaceae/Caesalpinioideae	*Prioria balsamifera*	Ntola blanc	192	CAN
Fabaceae/Caesalpinioideae	*Prioria oxyphylla*	Kalakati / Ntola rouge	50	CAN
Anacardiaceae	*Pseudospondias microcarpa*	Nzuza	25	CAN
Rubiaceae	*Psychotria dermatophylla*	Mbolo	36	UND
Rubiaceae	*Psydrax palma*	Mbuta	20	UND
Combretaceae	*Pteleopsis hylodendron*	Nkanza	91	CAN
Fabaceae/Faboideae	*Pterocarpus tinctorius*	Nkula	38	CAN
Myristicaceae	*Pycnanthus angolensis*	Lomba	21	CAN
Simaroubaceae	*Quassia undulata*	Vonda kadi	18	UND
Euphorbiaceae	*Ricinodendron heudelotii*	Nsanga Nsanga	46	CAN
Burseraceae	*Santiria trimera*	Pangi safu	5	UND
Olacaceae	*Schrebera trichoclada*	Kiala	3	UND
Flacourtiaceae	*Scottellia klaineana*	Sikoti	26	UND
Bignoniaceae	*Spathodea campanulata*	Mukela kusu	3	CAN
Anacardiaceae	*Spondias monbin*	Mungiengie	6	UND
Myristicaceae	*Staudtia kamerunensis*	Sunzu-menga	31	CAN

(continued)

Appendix (continued)

Sterculiaceae	*Sterculia bequaertii*	Tumba	38	CAN
Olacaceae	*Strombosia grandifolia*	Nkambu Kazi	53	UND
Olacaceae	*Strombosia pustulata*	Pangi Ya Kambu Kazi	3	CAN
Clusiaceae	*Symphonia globulifera*	Muangu-muangu	6	CAN
Myrtaceae	*Syzygium* sp.	Nkizu	1	UND
Apocynaceae	*Tabernaemontana crassa*	Kenge vumba	11	UND
Combretaceae	*Terminalia superba*	Limba	184	HEL
Euphorbiaceae	*Tetrorchidium didymostemon*	Tsudi Ba Ndumba	7	UND
Fabaceae/Mimosoideae	*Tetrapleura tetraptera*	Kiaka	7	UND
Sapotaceae	*Tieghemella heckelii*	Tsania nkazu	1	CAN
Moraceae	*Treculia africana*	Niania nzanza	3	UND
Anacardiaceae	*Trichoscypha acuminata*	Mfuta mfuta	7	UND
Rubiaceae	*Tricalysia crepiniana*	Fulututu	3	UND
Meliaceae	*Trichilia gilgiana*	Pangi soko	55	UND
Moraceae	*Trilepisium madagascariense*	Nsekene	23	CAN
Meliaceae	*Trichilia monadelpha*	–	9	UND
Anacardiaceae	*Trichoscypha oddonii*	Mbombolo	7	UND
Meliaceae	*Trichilia prieureana*	Bula Pembe	27	UND
Asteraceae	*Vernonia conferta*	Vukuvuku ya finda	7	UND
Verbenaceae	*Vitex welwitschii*	Filulongo	26	UND
Annonaceae	*Xylopia aethiopica*	Mukala	45	UND
Annonaceae	*Xylopia chrysophylla*	Likungu	51	UND
Annonaceae	*Xylopia wilwerthii*	Bengedele	120	UND
Rutaceae	*Zanthoxylum gilletii*	Nungu nsende	40	UND
Sapindaceae	*Zanha golungensis*	Pensi pensi	21	UND
Rutaceae	*Zanthoxylum* sp.	Nungu tsende	3	UND
Rutaceae	*Zanthoxylum welwitschii*	Dibelekete	5	UND