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Spatial and temporal variations in leaf area index, specific leaf area and leaf nitrogen of two co-occurring savanna tree species

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Summary Foliage growth, mass- and area-based leaf nitrogen concentrations (N_m and N_a) and specific leaf area (SLA) were surveyed during a complete vegetation cycle for two co-occurring savanna tree species: *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth. and *Cussonia arborea* A. Rich. The study was conducted in the natural reserve of Lamto, Ivory Coast, on isolated and clumped trees. Leaf flush occurred before the beginning of the rainy season. Maximum leaf area index (LAI), computed on a projected canopy basis for individual trees, was similar (mean of about 4) for both species. Seasonal courses of the ratio of actual to maximum LAI were similar for individuals of the same species, but differed between species. For *C. febrifuga*, clumped trees reached their maximum LAI before isolated trees. The LAI of *C. arborea* trees did not differ between clumped and isolated individuals, but maximum LAI was reached about 2 months later than for *C. febrifuga*. Leaf fall was associated with decreasing soil water content for *C. arborea*. For *C. febrifuga*, leaf fall started before the end of the rainy period and was independent of changes in soil water content. These features lead to a partial niche separation in time for light resource acquisition between the two species. Although N_m, N_a and SLA decreased with time, SLA and N_a decreased later in the vegetation cycle for *C. arborea* than for *C. febrifuga*. For both species, N_a decreased and SLA increased with decreasing leaf irradiance within the canopy, although effects of light on leaf characteristics did not differ between isolated and clumped trees. Given relationships between N_a and photosynthetic capacities previously reported for these species, our results show that *C. arborea* exhibits higher photosynthetic capacity than *C. febrifuga* during most of the vegetation cycle and at all irradiances.

Keywords: Crossopteryx febrifuga, Cussonia arborea, LAI, Lamto, phenology, shading, SLA.

Introduction

An important degree of regulation over transpiration and CO_2 assimilation occurs at the leaf surface (Sellers et al. 1997). Therefore, leaf phenology, defined here as the pattern and extent of variation of plant leaf area during a vegetation cycle, strongly influences carbon and water fluxes between vegetation and the atmosphere (Kikuzawa 1995), and interactions among individual plants and among plant species (Lechowicz and Koike 1995). Leaf phenology is affected by leaf type (deciduous and evergreen) and by environmental factors such as photoperiod, temperature (Hunter and Lechowicz 1992), water status (Borchert 1994, Eamus 1999) and atmospheric CO_2 concentration ($[CO_2]$) (Koike 1995). Concurrent with phenology, leaf carbon and water fluxes are determined by foliage properties. The amount of nitrogen per unit leaf area (N_a; g N m^{-2}) influences leaf photosynthetic capacity (Field and Mooney 1986), whereas specific leaf area (SLA, the leaf area to leaf mass ratio; $cm^2\ g^{-1}$) is an index of dry matter investment per unit leaf area. Both N_a and SLA generally decrease with leaf age (Reich et al. 1992, Wilson et al. 2001) and acclimate to leaf radiation microclimate (Gulmon and Chu 1981, Ellsworth and Reich 1992). This acclimation can occur within a plant canopy (Le Roux et al. 1999, 2001), and is viewed as a mechanism to adjust N_a to the leaf radiation microclimate.

Many studies have quantified spatial and temporal variations in leaf area index (LAI; m^2 leaf m^{-2} ground) and leaf characteristics in forest ecosystems (e.g., Pierce and Running 1988, McWilliam et al. 1993, Reich et al. 1999). For savanna ecosystems, data on phenology and leaf characteristics of the dominant tree species are scarce (but see Pressland 1975). This is of particular concern, because savannas cover about 20% of the global terrestrial surface (Scholes and Hall 1996), and the lack of information for this biome is recognized as a limitation in the development of models of climate change (Canadell et al. 2000, House et al. 2004). This knowledge gap also greatly restricts our ability both to assess water and carbon fluxes for the savanna biome and to understand competitive interactions between the main coexisting species of the tree layer in savanna ecosystems.

This lack of data for savanna trees is probably associated with the spatially heterogeneous structure of savanna vegetation (a discontinuous tree layer above a continuous grass layer). Surveys of tree leaf area are particularly tedious and time-consuming in these areas, because nondestructive methods of measuring LAI (based on remote sensing, e.g., Gamon et al. 1995, or radiation interception by foliage, e.g., Gower and Norman 1991) developed for closed canopies cannot be applied to heterogeneous canopies. In savanna ecosystems, several dominant tree species can coexist (e.g., Menaut and César 1979), with the additional feature of variable tree clumping (i.e., isolated trees and more or less dense clumps of trees).

The objectives of our study were to determine (1) whether temporal dynamics of leaf area, mass- and area-based leaf N concentrations (N_m and N_a, respectively) and SLA differ between two dominant tree species of the savanna of Lamto, Ivory Coast, and, within each species, between isolated trees and clumped trees; (2) whether leaf area dynamics are strongly related to soil water content dynamics; and (3) whether acclimation of leaf traits to the leaf radiation microclimate is an important mechanism for species belonging to sparse canopy systems, and whether it differs between species and between isolated trees and clumped trees. We surveyed the spatial and temporal variability of individual-tree LAI, SLA, N_m and N_a for two coexisting and dominant tree species, *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth. and *Cussonia arborea* A. Rich. (formerly *Cussonia barteri*). Both isolated and clumped trees were studied during one vegetation cycle. Leaves were collected from the same trees throughout the year at two contrasting irradiances, and N_a and SLA were calculated. Concurrently, soil water content was measured at different depths in the same locations. At one date during the year, N_m, N_a, SLA and sky openness (an index of radiation microclimate) were measured at different locations in the tree crowns. Implications for seasonal and spatial variations in tree carbon assimilation potential and for competitive interactions between individual trees are discussed.

Materials and methods

Study area and plant material

Measurements were conducted in the natural reserve of Lamto, Ivory Coast (6°13′ N, 5°02′ W). Mean monthly temperatures are constant throughout the year (27 °C). Rainfall averages 1200 mm year^{-1} unevenly divided between dry seasons (from December to February, and in August) and rainy seasons (from March to July, and from September to November). Soils are ferralsol (FAO classification). Fire is set every year in early January. Main features of the vegetation are described in Menaut and César (1979). Forests are present along streams, but most of the reserve corresponds to savanna areas. In the savanna, the herbaceous layer comprises perennial grasses. Tree density varies from almost pure grassland in bottomlands to dense shrubbery on plateaus.

The four dominant tree species include *C. febrifuga* and *C. arborea*, which can be found aggregated in clumps or isolated. The maximum height of these species is about 10–12 m. Roots of *C. arborea* extract water from deeper soil horizons than those of *C. febrifuga* (Le Roux and Bariac 1998). *Cussonia arborea* has a higher photosynthetic nitrogen-use efficiency than *C. febrifuga* (Simioni 2001).

Trees for this study were chosen in an area of about 1 ha presenting similar soil conditions and species composition. Within this study area, trees were either isolated or found within two dense clumps of mixed tree species. The field site was 150 m from the Lamto geophysical station, where daily climate data are routinely measured.

Estimation of LAI

The LAI survey was carried out during the 2000 vegetative cycle from January 2000 to January 2001. Five isolated and two clumped *C. febrifuga* trees (one tree per clump) and four isolated and three clumped *C. arborea* trees were studied (two trees from one clump plus one tree from the other clump). Trees were chosen to include young and reproductively active mature trees; tree height ranged from 1.85 to 6.8 m for *C. febrifuga*, and from 4 to 6.8 m for *C. arborea*.

Estimation of LAI was based on three measurements: (1) a survey of leaf number for two representative leaf clumps (i.e., growth units), one sun-exposed and the other shaded, for each tree during the whole 2000 vegetation cycle; (2) measurement of the total number of leaf clumps in each tree, including their spatial location in the canopy, at one date during the year; and (3) a survey of individual leaf area to convert leaf numbers to total leaf area. For each leaf clump, leaf number was counted every 2 weeks from January to April and from October to December, and every 4 weeks from May to September.

For each species, we searched for an estimator of leaf number in leaf clumps. Preliminary measurements made in 1999 suggested that good correlations exist between leaf number and basal diameter (BD) of the branch supporting the leaf clump for *C. febrifuga*, and between leaf number and the length of the foliated part of the supporting branch (LSB) for *C. arborea* (data not shown). These parameters were monitored on each surveyed leaf clump during the 2000 vegetation cycle to obtain precise relationships. Correlations at different periods of the 2000 vegetation cycle are presented in the Appendix.

On one day during the year (from May to October 2000, depending on the tree), we measured BD or LSB (depending on tree species) of all leaf clumps of each tree. On the basis of BD/LSB–green leaf number relationships, we estimated total leaf number per tree at one date in the vegetation cycle. For each tree, the ratio of total number of leaves to number of leaves of the surveyed clumps was assumed to be constant throughout the vegetation cycle. This allowed extrapolation of the temporal dynamics of total leaf number for each tree.

Estimates of mean leaf area were necessary to convert leaf numbers to total leaf area. Three times during the year (March 26, May 21 and October 23, 2000), eight leaf clumps were collected from four trees per species, and mean individual leaf areas were measured with a leaf area meter (Delta T Devices, Hoddeston, U.K.). Relationships between leaf individual areas and time (Figure 1) allowed conversion of total leaf number per tree to total leaf area.

To calculate individual tree canopy cover and tree height, all leaf clumps on each tree were located in space at the same time as total leaf clump BD/LSB relationships were measured. A reference point and a reference direction were chosen. Each leaf clump base was positioned by measuring the distance from the leaf clump to the reference point, the height of the leaf clump base and the angle made by the leaf clump base, the reference point, and the reference direction. Angles were measured with a large 0–90° protractor, with a precision of 0.1°. Distance was measured with a measuring tape, and height with a measuring tape used as a plumb line. Tree height was computed as the height of the highest leaf clump base plus 50 cm (to account for typical leaf clump dimensions). Canopy cover (i.e., projected area of the tree canopy) was computed as the horizontal surface delimited by the outer leaf clump positions, plus a margin of 50 cm, to account for the size of leaf clumps. Finally, individual-tree LAI was calculated as the ratio of total leaf surface to projected tree canopy cover.

Because measurements of leaf area were made on the same individuals, statistical techniques that include within-individual correlation between measurements were employed. A mixed model is recommended for this purpose. However, the shape of the time profile of LAI was complex and would have required at least four parameters (a cubic polynomial function of time) just to handle the time effect, which, given the size of our sample (14 trees), prevents testing the species and environment effects. We therefore performed a repeated measures analysis of covariance with time, species and environment (clump/isolated) as factors. All statistical analyses were performed with SAS software (SAS Institute, Cary, NC).

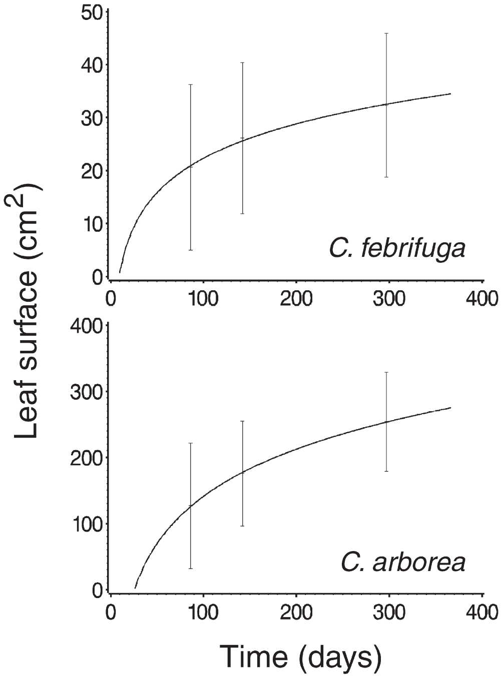

Figure 1. Temporal variations in mean individual leaf surface area for *Crossopteryx febrifuga* and *Cussonia arborea* during the 2000 vegetation cycle. Solid lines are best regression fits ($P < 0.05$) through mean individual leaf areas calculated from sampling all leaf age classes. Bars represent standard deviations.

To document the reproductive phenology of the species, the presence of flowers and fruits was recorded at each date of the LAI survey.

Leaf sampling and analysis and estimation of photosynthetic capacity

For each species, leaves were collected from two of the isolated trees and two of the clumped trees that were used for the LAI survey, every month at the beginning of the vegetation cycle, and every 2 months thereafter. For each tree, two sun leaves and two shade leaves were collected on different branches from those used for the survey of leaf clumps. Leaf surface was measured with a leaf area meter (Delta T Devices). Leaves were dried for 3 days at 70 °C and weighed. We calculated SLA as the ratio of leaf surface to leaf dry mass. Dried leaves were ground to pass a 0.08-mm mesh and N_m was measured with an elemental analyzer (NA 1500 Series 2, Fisons Instruments, Beverly, MA).

Parameters SLA, N_m and N_a were expressed against the time elapsed since leaf emergence, so measurements do not appear on the same dates for all trees. Because measurements were made on the same trees, at least two factors must be treated as repeated measures: time and exposition. However, because of the different dates, repeated measures ANOVA was inappropriate. We therefore used a mixed model: a variance/covariance model together with a covariance analysis model for fixed effects.

For the covariance analysis model (fixed effects), log-transformed N_m, N_a and SLA were the dependant variables, with species, tree environment (clumped, isolated) and leaf type as factors, and time as covariate. To avoid biased results because of the 16 parameters involved, and because most parameters were nonsignificant, we eliminated the most nonsignificant parameter and repeated the analysis. This procedure was repeated until only six parameters remained.

For the covariance model (random effects), we specified an autoregressive covariance model for time (AMR(1) model), based on the common observation that the correlation between observations with time decreases with the time lag. We also included a simple compound symmetry model for which we specified an individual-level variance and a constant correlation between sun and shade leaves within a tree. These two models allowed us to specify a different pattern of correlation between measurements taken on the same individual, according to time and leaf type.

We used relationships between maximum carboxylation rate (V_{cmax}; μmol CO$_2$ m^{-2} s^{-1}), at a leaf temperature of 31 °C, and N_a to illustrate contrasts in photosynthetic capacity caused by variations in N_a. For both tree species, the N_a–V_{cmax} relationships were in the form:

$$V_{cmax} = \frac{e^{c - \Delta H_a / RT_l}}{1 + e^{(\Delta S T_l - \Delta H_d)/RT_l}} \qquad (1)$$

where T_l is leaf temperature and c is a parameter defined as (Simioni (2001), for $T_l = 31$ °C):

$c = 50.226 + 0.996 \ln N_a$ for *C. febrifuga*, and

$c = 50.546 + 0.988 \ln N_a$ for *C. arborea.*

Other parameters are from Harley et al. (1992).

Hemispherical photographs

To characterize the influence of leaf radiation microclimate on SLA and N_a, hemispherical photographs were taken during October 16–26, 2000. We chose 21 leaves for *C. febrifuga* and 20 leaves for *C. arborea* on various isolated and clumped trees that were not surveyed for LAI to encompass a wide range of radiation regimes. Just above each leaf, a photograph was taken skyward with a Canon fish-eye 7.5-mm lens. Leaf mass, surface and N_m were analyzed as described above. An index of sky openness corresponding to percent of sky directly visible from the leaf (i.e., from the camera position) was computed from each hemispherical photograph with GLA software (Gap Light Analyzer Version 2.0, Fraser et al. 1999). Analysis of variance was used to determine effects of sky openness, environment (clump or isolated tree) and species on SLA and N_a.

Soil water content

Soil water was determined gravimetrically in the same area as the LAI survey. Measurements were made at four points out of tree cover and at four points under clumped trees. Because soil water contents in savannas are generally higher under tree cover than in the open (Scholes and Archer 1997), measurements in the open provided an estimate of the lowest soil water contents to which trees might be subjected. At each location, soil samples were collected at eight depths (0 to 160 cm in 20-cm intervals). Each sample was weighed, dried for 3 days at 100 °C, and reweighed. Difference between fresh and dry masses allowed calculation of soil water content as a percent. This value was converted to mm, assuming an apparent soil density of 1.5 kg kg^{-1} (Le Roux 1995). Soil water contents from the different layers were summed to compute soil water contents in the 0–60 cm and 60–160 cm horizons, to which tree water uptake behaviors were previously related (Le Roux and Bariac 1998). Conversions between soil water content in the 0–60-cm layer and shoot water potential of each species were made according to Le Roux and Bariac (1998).

Because soil water was measured in the same areas over time and there were some missing values, we analyzed the data with a mixed model assuming that the correlation between measurements in the same area decreases with time. The factors analyzed were time and environment (clump, open), and a separate analysis was performed for each soil horizon.

Results

Seasonal dynamics of LAI and soil water content

Leaf area index varied between trees of the same species. Maximum LAI (LAI_{max}) ranged from 2 to 7.4 with a mean of 4.2 for *C. febrifuga* and from 2.2 to 5.6 with a mean of 4.0 for *C. arborea*. Maximum LAI and tree height or canopy cover were uncorrelated. Because some trees had hollow stems, too few data were available to test the relationship between LAI_{max} and stem diameter. Mean annual LAI was 2.4 and 2.27 for isolated and clumped *C. febrifuga* trees, respectively, and 2.16 and 2.08 for isolated and clumped *C. arborea* trees, respectively.

Leaf area development (i.e., seasonal course of actual $\text{LAI}/\text{LAI}_{max}$) was homogeneous within species and tree cover type (Figures 2a and 2b). The seasonal course of LAI was significantly influenced by species and environment, and there was a significant interaction between time, species and environment (Table 1). There was a significant interaction between time and environment on LAI for *C. febrifuga*, but not for *C. arborea* (data not shown) (cf. Figure 2). For *C. febrifuga*, LAI increased and decreased earlier for clumped trees than for isolated trees. *Cussonia arborea* reached LAI_{max} about 2 months later than *C. febrifuga*. For both species, leaf fall started shortly after LAI_{max} was reached.

Soil water content in the top (0–60 cm) soil layer was high at the beginning of the year, as a result of rain in January, but decreased steeply afterward before the soil was replenished during the rainy season (Figure 2c). Soil water content decreased again after Day 300 when the dry season started. Soil water content in the 60–160 cm layer also decreased during the dry season and increased during the rainy season, but with less amplitude than in the upper layer, and more spatial variability at each date (Figure 2d). Soil water content was unaffected by the presence of tree clumps, except during the long dry season (between Day < 100 and Day > 300) in the 0–60 cm soil layer (Figures 2c and 2d). Statistical analysis (Table 2) yielded significant covariance components (overall likelihood ratio tests for top soil: χ^2 (1 df) = 4.38, $P = 0.0363$; for deep soil: χ^2 (2 df) = 40.44, $P < 0.0001$), indicating that the data are not independent over time. There was no significant effect of environment on soil water content, but there was a significant interaction between time and environment for the top soil layer, indicating that variations in soil water content with time were different in the open and under tree cover. This confirms the patterns observed in Figure 2.

Crossopteryx febrifuga and *C. arborea* trees started leaf growth when soil water content was low and precipitation was scarce. *Crossopteryx febrifuga* leaf fall did not coincide with declining soil water content, at least for clumped trees, whereas the rapid leaf fall in *C. arborea* corresponded to a steep decrease in soil water contents in all soil layers.

Reproductive phenology

The flowering period ranged from February to May for *C. febrifuga* trees and from April to May for *C. arborea* trees. *Cussonia arborea* trees produced fruits from May to August;

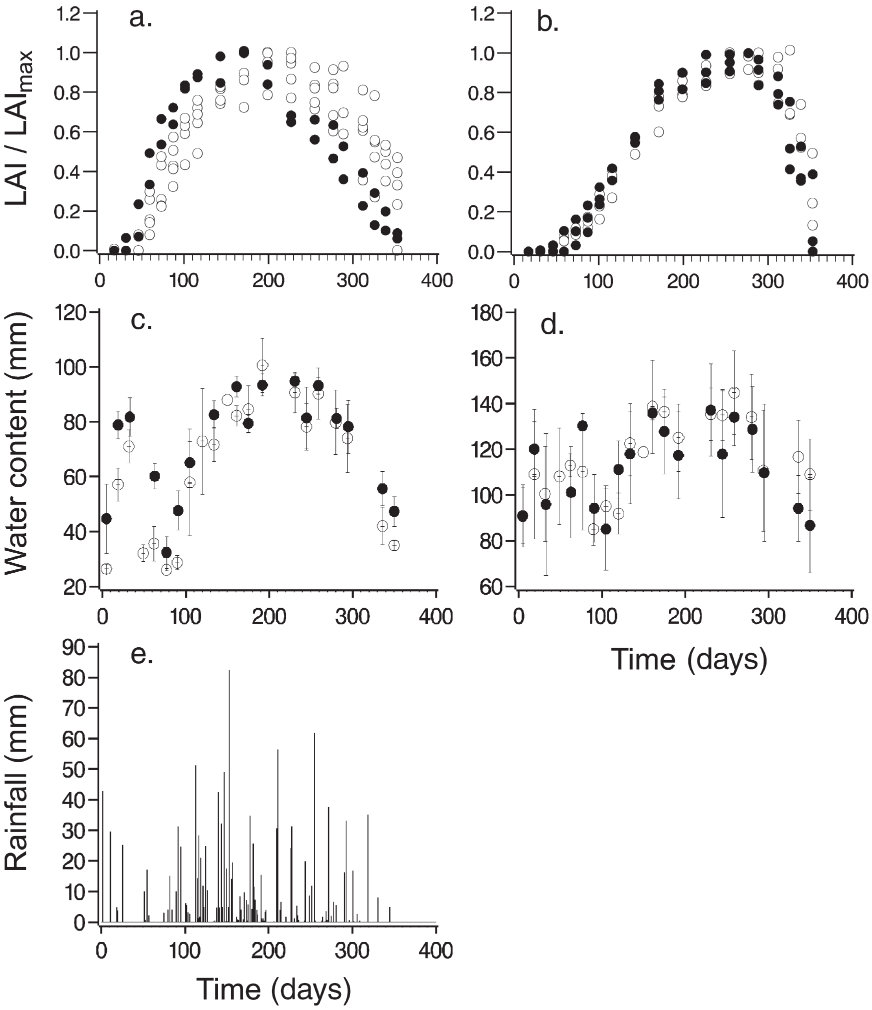

Figure 2. Temporal dynamics of individual tree leaf area index, soil water content and daily rainfall during the 2000 vegetation cycle. (a) Leaf area index (expressed as the ratio of actual (LAI) to maximum (LAI$_{max}$) leaf area indices) of *Crossopteryx febrifuga* for five isolated (○) and two clumped (●) trees. (b) Leaf area index of *Cussonia arborea* for four isolated (○) and three clumped (●) trees. (c) Soil water content in the 0–60-cm soil layer in open areas (○) and under tree clumps (●); bars represent standard deviations. (d) Soil water content in the 60–160-cm soil layer. (e) Daily rainfall.

after this period, no more fruits remained on the trees. Fruit growth started in April for *C. febrifuga*, and fruits remained on the trees until the end of the year, making it difficult to determine precisely when maximum fruit growth was achieved.

Temporal and spatial variations of N_m, N_a, SLA and V_{cmax}

Values of N_m, N_a and SLA decreased after leaf growth initiation (Figures 3 and 4). The decrease in N_m was steep shortly after leaf initiation and less pronounced after Day 100 for *C. febrifuga*, whereas the decrease was much more progressive for *C. arborea*. A weak decrease in N_a of *C. febrifuga* was observed shortly after leaf initiation, and then N_a remained quite constant. In contrast, N_a of *C. arborea* was constant during the first 100 days and decreased sharply from Day 150 to Day 300. In both species, SLA decreased nonlinearly, but the decrease was larger for *C. febrifuga* than for *C. arborea*. For all variables, the overall variance/covariance model was significant (null model likelihood ratio test: for SLA, χ^2 (3 df) = 29.40; for N_m, χ^2 (2 df) = 23.41; and for N_a, χ^2 (2 df) = 26.41; all $P < 0.0001$). The significant interaction between tree and exposition in the random effects covariance model showed that there was a significant effect of exposition at the tree level.

Mass-based leaf N concentration was influenced by time since bud break and differed significantly between species (higher for *C. arborea* than for *C. febrifuga*), and between leaf types within species (Table 3). Leaf type influenced N_m of *C. arborea* (being higher for sunlit leaves than for shaded leaves) but not for *C. febrifuga* (data not shown). In addition, the temporal variation in N_m differed between species (Table 3).

Specific leaf area was influenced by time since bud break, by species (higher for *C. arborea* than for *C. febrifuga*), by environment (higher for clumped trees than for isolated trees) and by leaf type (higher for shaded leaves than for sunlit

Table 1. Summary of repeated measure analysis of variance for relative leaf area index.

Source of variation	df	SS	*F*	*P*
Time	18	41.254	78.41	< 0.0001
Time × species	18	10.964	20.84	< 0.0001
Time × environment	18	3.008	5.72	< 0.0001
Time × species × environment	18	1.956	3.72	< 0.0001
Error	162	4.735		

Table 2. Summary of mixed analysis of variance (SAS Institute, PROC mixed) of effects of time and environment (tree clump or open area) on soil water content.

Horizon	Variance component	Estimate	SEM	*P*
Top soil	Rho	1.000	0.000	
	Gamma	0.200	0.180	0.2703
	Residual	45.764	13.400	0.0003
Deep soil	Rho	0.986	0.018	< 0.0001
	Gamma	0.792	0.140	< 0.0001
	Residual	278.92	148.77	0.0594
	Fixed effects	df	*F*	*P*
Top soil	Intercept	1,3	1969.0	< 0.0001
	Environment	1,3	7.8	0.0686
	Time	17,3	40.2	< 0.0001
	Environment × time	17,3	2.3	0.0206
Deep soil	Intercept	1,3	304.0	0.0004
	Environment	1,3	0.2	0.6945
	Time	17,3	11.4	< 0.0001
	Environment × time	17,3	1.4	0.2051

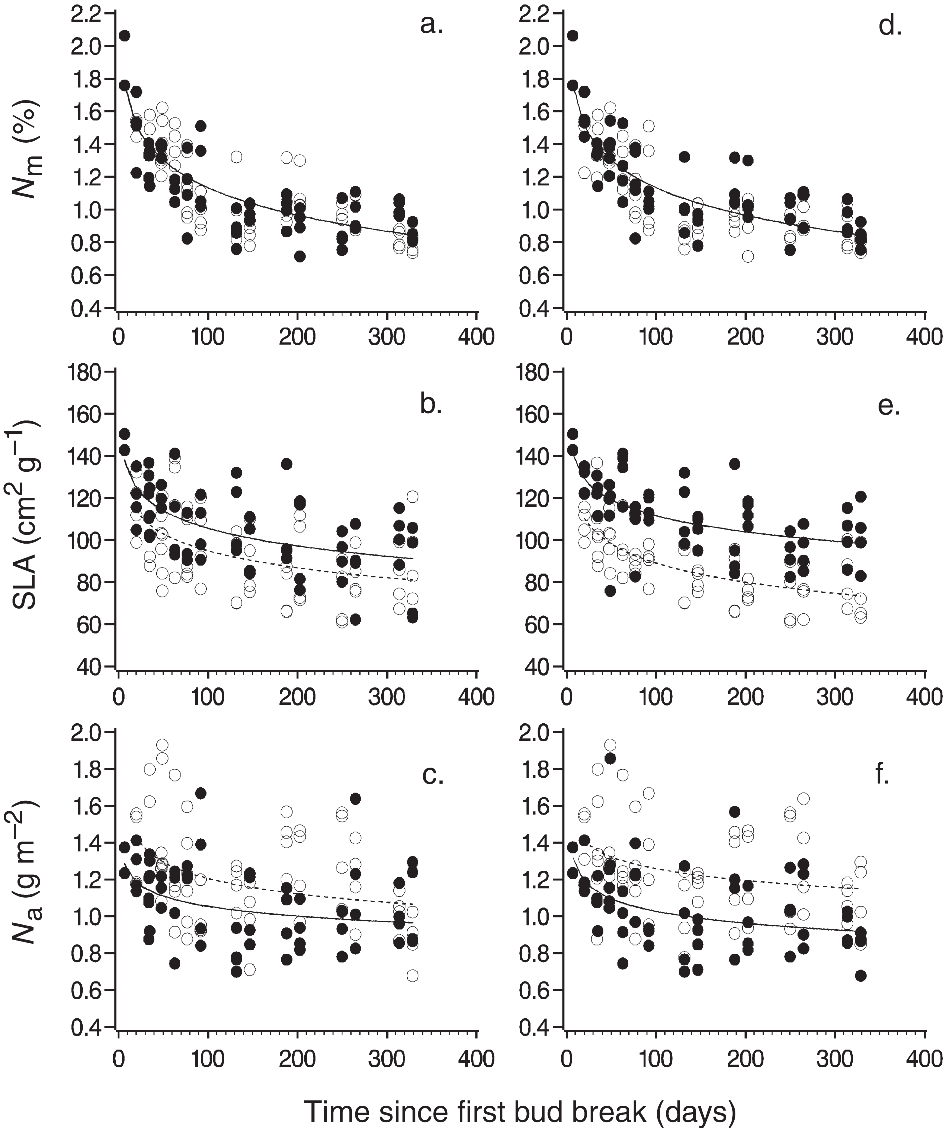

Figure 3. Temporal dynamics of (a, d) leaf nitrogen concentration per unit mass (N_m), (b, e) specific leaf area (SLA) and (c, f) leaf nitrogen concentration per unit leaf area (N_a) of *Crossopteryx febrifuga*, since first leaf emergence. Open and closed symbols correspond to isolated and clumped trees (a, b and c) and sunlit and shaded leaves (d, e and f), respectively. Solid lines represent best significant regression fits with time for either clumped trees or shaded leaves, and dashed lines represent best regression fits for either isolated trees or sunlit leaves ($P < 0.05$).

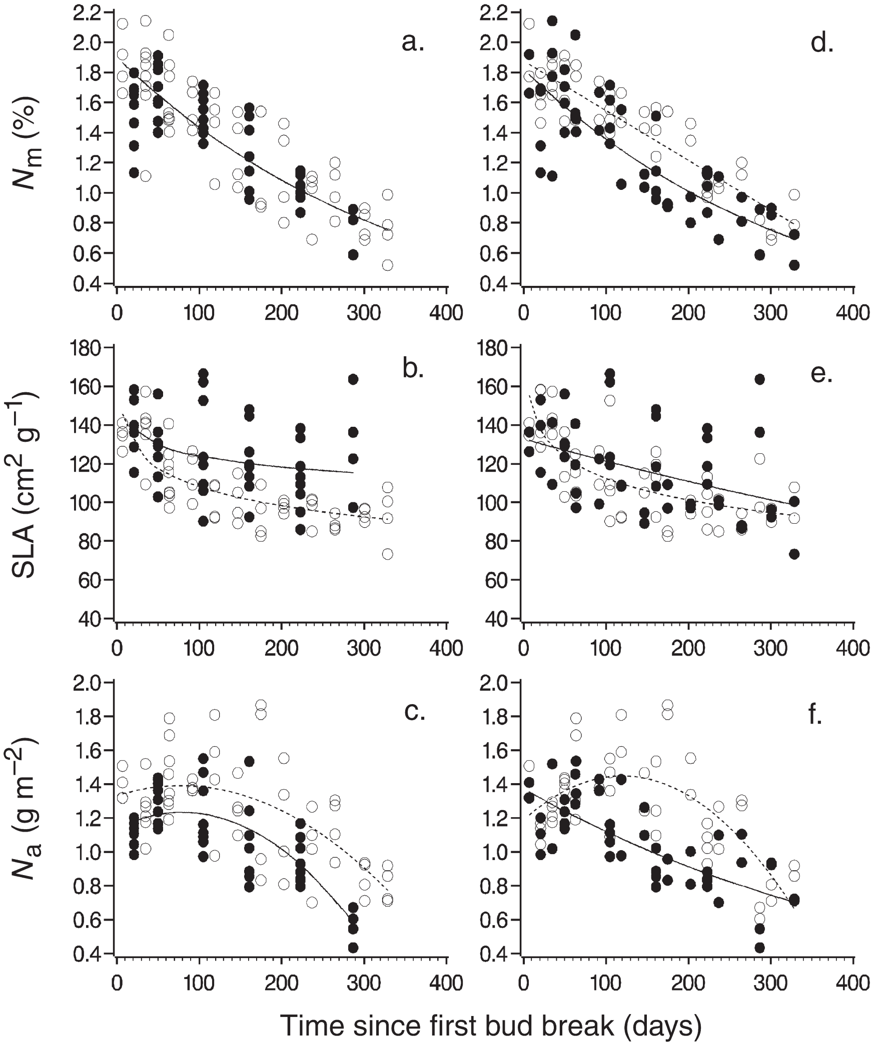

Figure 4. Temporal dynamics of (a, d) leaf nitrogen concentration per unit leaf mass (N_m), (b, e) specific leaf area (SLA) and (c, f) leaf nitrogen concentration per unit leaf area (N_a) of *Cussonia arborea*, since first leaf emergence. Open and closed symbols correspond to isolated and clumped trees (a–c) and sunlit and shaded leaves (d–f), respectively. Solid lines represent best significant regression fits with time for either clumped trees or shaded leaves, and dashed lines represent best regression fits for either isolated trees or sunlit leaves ($P < 0.05$).

leaves) (Table 4). Variations with leaf type differed between species.

Area-based leaf N concentration varied significantly with time (variation with time differed between species), species (higher for *C. arborea* than for *C. febrifuga*), environment (higher for isolated trees than for clumped trees) and leaf type

Table 3. Summary of mixed analysis of variance (SAS Institute, PROC mixed) of effects of time, species, tree environment (clump or isolated tree) and leaf type (sunlit or shaded) on leaf nitrogen concentration per unit dry mass.

Covariance model (variance components):	Covariance parameter	Subject	Estimate	SE	Z value	Prob Z
	Variance	Tree	0			
	CS	Tree	–0.00120	0.000446	–2.69	0.0072
	AMR(1)	Tree × leaf type	0.3363	0.07061	4.76	< 0.0001
	Residual		0.02655	0.003002	8.84	< 0.0001

Covariance analysis (fixed effects):	Effect	df	*F*	*P*
	Intercept	1,11	499.26	< 0.0001
	Time	1,202	259.65	< 0.0001
	Species	1,202	46.10	< 0.0001
	Environment	1,202	1.17	0.2814
	Species × leaf type	2,202	4.37	0.0138
	Time × species	1,202	16.11	< 0.0001

Table 4. Summary of mixed analysis of variance (SAS Institute, PROC mixed) of effects of time, species, tree environment (clump or isolated tree) and leaf type on specific leaf area.

Covariance model (variance components):	Covariance parameter	Subject	Estimate	SE	Z value	Prob Z
	Variance	Tree	0.003292	0.003347	0.98	0.1626
	CS	Tree	–0.00079	0.001992	–0.40	0.6912
	AMR(1)	Tree × leaf type	0.2988	0.09098	3.28	0.0010
	Residual		0.01639	0.002054	7.98	< 0.0001

Covariance analysis (fixed effects):	Effect	df	*F*	*P*
	Intercept	1,11	46664.4	< 0.0001
	Time	1,200	74.56	< 0.0001
	Species	1,200	26.43	< 0.0001
	Environment	1,200	16.84	< 0.0001
	Leaf type	1,11	14.59	0.0028
	Species × leaf type	1,200	6.07	0.0146

(higher for sunlit leaves than for shaded leaves) (Table 5).

Estimated V_{cmax} varied with time and was higher for *C. arborea* than for *C. febrifuga*, except at the end of the vegetation cycle (Figure 5).

Effects of irradiance on N_m, N_a and SLA

Sky openness had no effect on N_m (data not shown). For both species, N_a increased and SLA decreased with increasing mean irradiance in October 2000 (Figure 6). No significant difference was found between isolated and clumped trees, except for a weak effect of irradiance on N_a (Table 6), but N_a was significantly higher for *C. febrifuga* and SLA significantly higher for *C. arborea*.

Discussion

Seasonal dynamics of LAI

The erratic individual tree LAI_{max}, observed for both species, was caused by variations in individual tree canopy shape, which can be influenced by tree growth environment (e.g., fire and neighbors). The lack of correlation between LAI_{max} and projected canopy cover, tree height or stem diameter was partly a result of the small number of trees sampled, and partly because half of the trees had hollow stems. However, the consistent temporal variations in the LAI/LAI_{max} ratio observed between trees within a species allowed accurate quantification of the periods of leaf growth and leaf fall.

Crossopteryx febrifuga and *C. arborea* initiated leaf growth under unfavorable soil water conditions. Soil water content at bud break in the 0–60-cm layer was between 35 and 80 mm for *C. febrifuga* and between 25 and 60 mm for *C. arborea*. These values correspond to predawn shoot water potentials between –0.7 and –0.2 MPa for *C. febrifuga* and between –0.5 and –0.2 MPa for *C. arborea* (Le Roux and Bariac 1998). In several deciduous tropical tree species, stem rehydration occurs before the onset of the rainy season, allowing leaf flushing toward the end of the dry season (Williams et al. 1997). In both

Table 5. Summary of mixed analysis of variance (SAS Institute, PROC mixed) of effects of time, species, tree environment (clump or isolated tree) and leaf type on leaf nitrogen concentration per unit leaf area.

Covariance model (variance components):	Covariance parameter	Subject	Estimate	SE	Z value	Prob Z
	Variance	Tree	0			
	CS	Tree	–0.00067	0.001286	–0.52	0.6015
	AMR(1)	Tree × leaf type	0.3785	0.07302	5.18	< 0.0001
	Residual		0.03546	0.004258	8.33	< 0.0001

Covariance analysis (fixed effects):	Effect	df	*F*	*P*
	Intercept	1,12	102.34	< 0.0001
	Time	1,198	61.65	< 0.0001
	Species	1,198	6.02	0.0150
	Environment	1,198	20.37	< 0.0001
	Leaf type	1,12	21.45	0.0006
	Time × species	1,198	12.18	0.0006

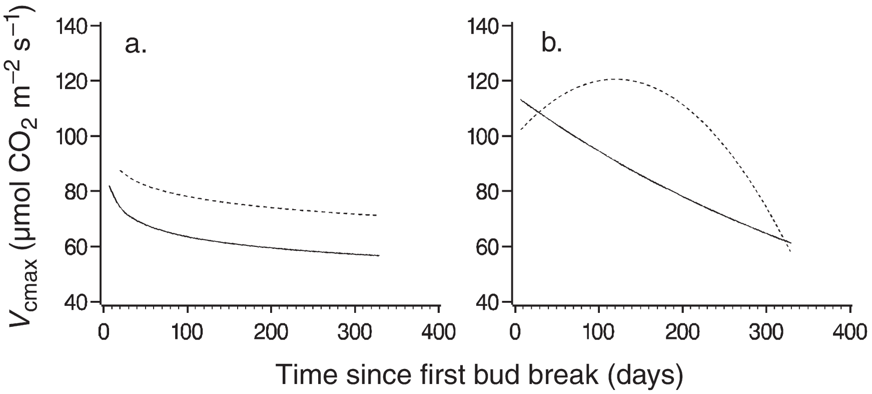

Figure 5. Estimated temporal dynamics of the maximum rate of carboxylation (V_{cmax}) at 31 °C for sunlit (dashed lines) and shaded (solid lines) leaves of (a) *Crossopteryx febrifuga* and (b) *Cussonia arborea*. We calculated V_{cmax} from relationships with N_a (Simioni 2001) and from regression fits of N_a with time (this study).

species, the time to reach maximum LAI$_{max}$ after first bud break was consistent with the leaf growth patterns of other deciduous tropical savanna species (Eamus 1999).

Leaf fall in *C. febrifuga* started early in the vegetation cycle before any decrease in soil water content, at least for clumped trees. Conversely, leaf shedding in *C. arborea* corresponded to a steep decrease in soil water contents in both horizons, suggesting that, for this species, once foliage development has started, it continues as long as water conditions are favorable. Williams et al. (1997) observed that, for all deciduous species in an Australian tropical savanna, leaf fall occurred concurrently with a decrease in soil water content. In the Lamto reserve, Konaté et al. (1998) observed that *C. febrifuga* trees growing on termite mounds (i.e., with higher soil water content) lost their leaves later than individuals growing on ordinary soil. However, we observed that clumped *C. febrifuga* trees, which experienced more favorable water conditions than isolated trees, started leaf fall before isolated trees, indicating that soil water content was not the only determinant of leaf shedding. Our results for *C. arborea* leaf shedding were in accordance with Konaté et al. (1998), who observed no difference in leaf shedding with soil type. *Cussonia arborea* may have access to a larger water pool than *C. febrifuga* (Le Roux and Bariac 1998), and thus more potential to build leaves later in the year.

There was a temporal segregation of leaf development between species. *Crossopteryx febrifuga* had high LAI values (> 0.7 LAI$_{max}$) from Days 100 to 250, whereas *C. arborea* had high LAI values from Days 180 to 300, leading to a partial niche separation in time for light resource acquisition between the species. Niche separation was particularly marked for *C. febrifuga* trees in clumps (which may be close to *C. arborea* trees); in these trees, foliage growth and leaf fall started earlier than in isolated *C. febrifuga* trees. It is unlikely that allocation to reproductive parts caused this separation, because both species flowered and produced fruits at about the same time.

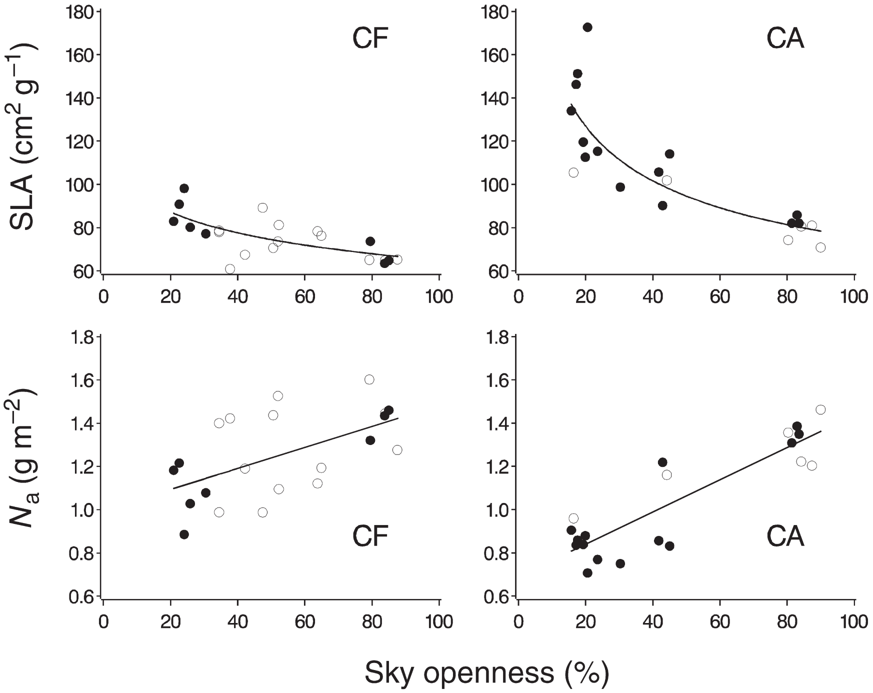

Figure 6. Effects of sky openness on specific leaf area (SLA) and leaf nitrogen concentration per unit leaf area (N_a) for *Crossopteryx febrifuga* (CF) and *Cussonia arborea* (CA). Measurements were made in October 2000, on isolated (○) and clumped (●) trees. Solid lines represent best significant regression fits ($P < 0.05$). Regression coefficients are 0.46 and 0.32 for CF SLA and N_a, and 0.74 and 0.78 for CA SLA and N_a, respectively.

Table 6. Summary of analysis of covariance (SAS Institute, PROC GLM) of effects of sky openness (open, % of sky visible from the leaf position), tree environment (clumped or isolated tree) and species on specific leaf area (SLA) and leaf nitrogen per unit leaf area (N_a). Sky openness was measured in October 2000, and leaves were sampled at the same time.

	Effect	df	F	P
SLA	Intercept	1	1656.3	< 0.0001
	Sky openness	1	42.75	< 0.0001
	Species	1	22.91	< 0.0001
	Environment	2	2.46	0.0989
N_a	Intercept	1	256.12	< 0.0001
	Sky openness	1	41.99	< 0.0001
	Species	1	12.05	0.0013
	Environment	2	3.71	0.0335

Seasonal variations in N_m, N_a, SLA and photosynthetic capacity

Both N_m and SLA declined with time, as generally observed during leaf expansion and aging (Field and Mooney 1983). Mass-based leaf N concentration was high in young expanding leaves, as observed for other species (Chapin and Kedrowski 1983, Millard and Nielsen 1989), and then decreased, probably as a result of incorporation of N in structural material, and eventually, as a result of N retranslocation during leaf senescence (Crane and Banks 1992, Norby et al. 2000). As a result, N_a declined with time. However, the time course of decline differed between *C. arborea* and *C. febrifuga. Cussonia arborea* maintained higher N_m and N_a values with time, particularly in sunlit environments. Given that *C. arborea* has a higher photosynthetic capacity at a given N_a, this allowed *C. arborea* trees to maintain high photosynthetic capacity later than *C. febrifuga*, as suggested by the estimated temporal variation in V_{cmax} (Figure 5). Along with the high LAI observed for *C. arborea* late in the vegetation cycle, this indicates that *C. arborea* was more photosynthetically active during the second half of the year than *C. febrifuga*, except at the end of the vegetation cycle.

Higher SLA can be advantageous for *C. arborea* because of the lower carbon investment in leaves. However, the high SLA of *C. arborea* does not account for the long petioles that contribute about 33% of total leaf mass (G. Simioni, unpublished data) and thus markedly increase carbon investment in leaves.

Within-canopy variations in N_m, N_a and SLA

Analysis of the seasonal dynamics of leaf traits showed that N_m differed between sunlit and shaded leaves of *C. arborea*. Although this suggests that more N was allocated to sunlit leaves than to shaded leaves, the suggestion was not confirmed by the analyses of N_m of leaves for which sky openness was measured.

Variation in N_a and SLA with the local leaf radiation regime (i.e., sky openness) was consistent with published results (Chabot et al. 1979, Gulmon and Chu 1981, Le Roux et al. 1999, Rijkers et al. 2000) and is interpreted as an important feature that increases light-use efficiency at the plant level (Field 1983, Hollinger 1996). Our results support the recommendations of Le Roux et al. (1999) and Rijkers et al. (2000) that optimization of tree carbon gain should be studied by analyzing patterns of investment in leaf dry mass per area rather than in N_m.

The correlation between SLA and sky openness was unaffected by tree type (isolated or clumped), which contrasted with the dynamics of SLA observed during the vegetation cycle. On the other hand, the effect of irradiance on N_a was in accordance with the seasonal survey. Although we followed the temporal dynamics of N_a and SLA of sunlit and shaded leaves on isolated and clump trees, we did not measure the irradiance on each leaf. It is likely, however, that a sun leaf on an isolated tree is exposed to a higher irradiance than a sun leaf on a clumped tree, and a shade leaf on a clumped tree is probably exposed to a lower irradiance than a shade leaf on an isolated tree. Such differences may explain why SLA and N_a differed between isolated and clumped trees in the temporal survey.

Sky openness was measured in October, when *C. febrifuga* LAI was below maximum. However, light conditions for leaves at very low (deeply shaded leaves) or very high (full sun leaves) sky openness indices were probably not greatly different from those prevailing during the period of LAI_{max}. Furthermore, it is these leaves that largely determine the relationships between SLA and sky openness, and between N_a and sky openness. In addition, even in the case of changes in light conditions, reacclimation of leaves to the new light conditions may have occurred (Frak et al. 2001). Thus, the difference in acclimation between the two species is unlikely to be biased by the date when the hemispherical photographs were taken.

Comparison with other species worldwide

Specific leaf areas of *C. febrifuga* and *C. arboria* are in the range of SLAs for deciduous trees, either temperate or tropical. However, compared with other deciduous tree species world wide (see reviews by Schulze et al. 1994, Reich et al. 1999), *C. febrifuga* and *C. arboria* have among the lowest leaf N concentrations recorded for deciduous species, more closely resembling values reported for evergreen trees. The infertile soil at Lamto may account for the low N_m and N_a values of *C. febrifuga* and *C. arborea*.

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Appendix

Leaf clump allometry

The following equations were used to predict green leaf numbers (n_{GL}) from basal diameters (BD; mm) of the supporting branch of leaf clumps for *Crossoteryx febrifuga* or from length of the supporting branch corresponding to leaf insertion (LSB; cm) for *Cussonia arborea*. All leaf clumps were measured between May and October for *C. febrifuga* trees, and in May and August for *C. arborea* trees. For *C. febrifuga*, for all leaf groups for which BD was below 4 mm, n_{GL} was estimated with a regression fit to data from all months with BD values < 4 mm.

Crossopteryx febrifuga:

May:	$n_{GL} = 26.58BD - 95.87$	$R^2 = 0.81$
June:	$n_{GL} = e^{2.18BD - 0.0774}$	$R^2 = 0.78$
August:	$n_{GL} = e^{2.484BD - 0.9675}$	$R^2 = 0.81$
October:	$n_{GL} = 11.93BD - 42.74$	$R^2 = 0.6$
BD < 4 mm:	$n_{GL} = e^{2.482BD - 0.625}$	$R^2 = 0.86$

Cussonia arborea:

May:	$n_{GL} = 1.148LSB + 15.0697$	$R^2 = 0.93$
August:	$n_{GL} = 1.189LSB - 17.158$	$R^2 = 0.88$