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Leaf area index from litter collection: impact of specific leaf area variability within a beech stand

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Abstract. Litter fall collection is a direct method widely used to estimate leaf area index (LAI) in broad-leaved forest stands. Indirect measurements using radiation transmittance and gap fraction theory are often compared and calibrated against litter fall, which is considered as a reference method, but few studies address the question of litter specific leaf area (SLA) measurement and variability. SLA (leaf area per unit of dry weight, $m^2 \cdot g^{-1}$) is used to convert dry leaf litter biomass ($g \cdot m^{-2}$) into leaf area per ground unit area ($m^2 \cdot m^{-2}$). We paid special attention to this parameter in two young beech stands (dense and thinned) in northeastern France. The variability of both canopy (closure, LAI) and site conditions (soil properties, vegetation) was investigated as potential contributing factors to beech SLA variability. A systematic description of soil and floristic composition was performed and three types of soil were identified. Ellenberg's indicator values were averaged for each plot to assess nitrogen soil content. SLA of beech litter was measured three times during the fall in 23 plots in the stands (40 ha). Litter was collected bimonthly in square-shaped traps (0.5 m^2) and dried. Before drying, 30 leaves per plot and for each date were sampled, and leaf length, width, and area were measured with the help of a LI-COR areameter. SLA was calculated as the ratio of cumulated leaf area to total dry weight of the 30 leaves. Leaves characteristics per plot were averaged for the three dates of litter collection. Plant area index (PAI), estimated using the LAI-2000 plant canopy analyser and considering only the upper three rings, ranged from 2.9 to 8.1. Specific leaf area of beech litter was also highly different from one plot to the other, ranging from 150 to 320 $cm^2 \cdot g^{-1}$. Nevertheless, no relationship was found between SLA and stand canopy closure or PAI. On the contrary, a significant relationship between SLA and soil properties was observed. Both SLA and leaf area had the lowest values in the most hydromorphic soil with the highest nitrogen content. On the other hand, the highest values of SLA and leaf area were observed on the plots with the lowest nitrogen content. This spatial variability of SLA was taken into account to estimate LAI from litter collected at eight plots. For our study site, we conclude that neglecting SLA spatial variability is at the source of 8–24% error in the calculation of LAI.

Résumé. La collecte de litière est une méthode largement employée pour estimer l'indice foliaire (LAI) des peuplements feuillus. Les méthodes indirectes basées sur l'inversion du modèle de Poisson de distribution des transmittances ou des fractions de trouées, sous sa forme simple ou modifiée, sont souvent calibrées et comparées à la collecte de litière, qui est considérée comme une méthode de référence. Peu d'études ont porté sur la mesure de la surface spécifique des feuilles de litière (« specific leaf area », SLA) et sa variabilité. Le SLA (surface de feuille par unité de masse, $m^2 \cdot g^{-1}$) est utilisé pour convertir la masse sèche des échantillons de feuilles ($g \cdot cm^{-1}$) en surface de feuilles par unité de surface de sol ($m^2 \cdot m^{-2}$). Nous avons apporté une attention particulière à ce paramètre dans un jeune peuplement de hêtre (dense et éclairci) dans le nord-est de la France. La variabilité de la structure de la canopée (ouverture du couvert, indice foliaire LAI) et des conditions locales du milieu (propriétés du sol, végétation) ont été investiguées comme facteurs pouvant potentiellement contribuer à la variabilité du SLA du hêtre. Une description systématique du sol et de la végétation herbacée a été réalisée, et trois types de sol ont été identifiés. Les coefficients ont été calculés sur chaque point afin d'estimer la quantité d'azote du sol disponible. Le SLA du hêtre a été estimé à trois reprises durant la chute des feuilles sur 23 placettes dans le peuplement (40 ha). La litière a été collectée toutes les deux semaines dans des bacs de 0,5 m^2 et séchée. Avant séchage, 30 feuilles par placette et par date ont été échantillonnées et les caractéristiques telles que longueur et surface élémentaire foliaire, ont été mesurées à l'aide d'un planimètre LI-COR. Le SLA est calculé comme le rapport de la surface cumulée des 30 feuilles sur leur masse. Les caractéristiques de feuilles ont été calculées en moyenne sur les trois dates de ramassage. L'indice foliaire, estimé à l'aide de l'analyseur du couvert LAI-2000 en conservant les trois anneaux supérieurs, varie entre 2,9 et 8,1. Le SLA de la litière du hêtre est également très variable d'un point de mesure à un autre, allant de 150 à 320 $cm^2 \cdot g^{-1}$. Néanmoins aucune relation n'a été trouvée entre le SLA et l'ouverture du couvert ou le LAI. Au contraire, une relation

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significative entre le SLA et les propriétés du sol a été observée. SLA et la surface élémentaire foliaire prennent les valeurs les plus faibles sur le type de sol le plus hydromorphe, possédant aussi la plus forte teneur en azote. A l'opposé, les plus fortes valeurs de SLA et de surface foliaire élémentaire ont été mesurées sur les placettes possédant la plus faible teneur en azote. La variabilité spatiale du SLA a été prise en compte dans le calcul du LAI à partir des collectes de litière sur huit placettes. Dans le cas de notre site, nous concluons que la non prise en compte de la variabilité spatiale du SLA est à la source d'erreurs allant jusqu'à 8–24 % dans le calcul ponctuel du LAI.

Introduction

It is now largely recognised that leaf area index (LAI), defined as the total one-sided area of leaves per unit ground surface area (Watson, 1947; Lang et al., 1991), is a key parameter describing canopy structure, driving both gas fluxes (water and CO_2) and energy. It has therefore been quantified in most forest ecophysiological experiments and is studied by itself, since it describes the canopy–atmosphere interface (Ehleringer and Field, 1993). The indirect methods used to estimate LAI on large areas or numerous plots are faced with problems of intrinsic assumptions violation, such as the non-randomness of the spatial distribution of leaves, and are for that reason often compared or calibrated against leaf litter collection for broad-leaved species (Chason et al., 1991; Dufrêne and Bréda, 1995). This commonly used approach consists of measuring leaf mass and calculating LAI from the ratio of leaf mass to leaf area (Aber, 1979). There are several ways to assess leaf mass, either by allometric relationships or by collecting leaf litter fall. Concerning this last method, the only assumption made is that the collectors obtain a random sample of the overlying leaves (Chason et al., 1991). The success of this direct method, especially for broad-leaved species, can be explained by the relatively moderate amount of labour involved. In this method, the total dry weight of leaves collected within traps of known dimensions is converted into area using a species-specific leaf area to dry weight ratio, specific leaf area (SLA, in $m^2 \cdot g^{-1}$). As the SLA determination is the harder step in the direct LAI measurement, it is generally determined on a subsample of collected leaves and is applied during the whole leaf-fall period or even for different years, as in the studies reported by Neumann et al. (1989) and Chason et al. (1991).

Few studies have examined the effects of in situ spatial and temporal variability of SLA on LAI estimation. However, it has been known for a long time that leaf morphological characteristics may change with resource availability (Jurik, 1986; Walters and Reich, 1989; Castro-Diez et al., 1997). In beech stands, Aussenac and Ducrey (1977) and Cermak (1998) reported a strong SLA vertical gradient that was related to the cumulated LAI profile from the top to the bottom of the crowns. The strong leaf differentiation resulting in morphological adaptation to available light leads to the determination of so-called sun and shade leaves already observed on several species (e.g., Abrams and Mostoller, 1995). At the largest scales, canopy SLA was reported to decrease with a decrease in water availability (Jose and Gillespie, 1997; Hobbie, 2000) or nutrient resource (Coyne and van Cleve, 1977). These results established on green leaves address the question of litter SLA variability. We hypothesized that such environmental effects may also be found on litter SLA, particularly those concerning soil conditions and canopy structure. The aims of our study are thus to (*i*) describe the spatial variability of beech SLA in two pure even-aged beech stands, (*ii*) identify the influences of both soil moisture or nutrient regime and stand canopy structure characteristics on SLA, and (*iii*) quantify the consequences of the observed variability on LAI calculated from litter collection.

Materials and methods

Site description

The study was conducted in the Hesse State Forest, located in the east of France in the eastern side of the plateau of Lorraine (48°40′N, 7°05′E, altitude 300 m above sea level). The climate is semicontinental, with average annual temperature of 9.2°C and average annual rainfall of 820 mm. The experimental site was composed of two adjoining stand management units named P217 and P218 covering 45 ha, treated as high forest. Both stand units have the same age (35 years) and are composed mainly of beech (*Fagus sylvatica* L.), which represents 75% of the total basal area, hornbeam (*Carpinus betulus* L.), sessile oak (*Quercus petraea* Matt. Liebl.), and silver birch (*Betula pendula* L.). Stand P217 was thinned by foresters during the winter of 1998–1999, resulting in the removal of 20–25% of the total basal area, mainly involving trees from the upper diameter classes. Stand density in 2000 was 4473 and 4957 $stems \cdot ha^{-1}$ for P217 and P218, respectively. The total basal area in the thinned stand P217 was 21.6 $m^2 \cdot ha^{-1}$, and dominant height ranged from 10.7 to 15.5 m (mean = 13.9 m). In the unthinned stand P218, total basal area was 23.9 $m^2 \cdot ha^{-1}$, and dominant height ranged from 7.2 to 16.4 m (mean = 13.7 m).

Soil and vegetation description

A systematic network of 182 plots measuring 50 × 50 m was created in 1998 to describe soil and understory vegetation within the stands (**Figure 1**). The centre of each plot was marked with a white stake. An exhaustive phytosociological relevé of species was carried out in 1999 within a circle of radius 12 m centred on each plot (plot area 452 m^2). The relevés were used to compute Ellenberg's indicator values (IV) at each plot (Ellenberg et al., 1992). Plot average IVs were calculated for the four cited factors as the mean of IVs given for every species present within the plot for which IV was not zero. Briefly, the Ellenberg IV provides quantitative estimates of soil factor influence on about 3000 vascular plants of Central Europe. The factors we considered in our analysis characterize soil nitrogen availability (N), soil moisture (F), soil reaction (R), and light (L). The IVs range from 1 to 9 (except 1 to 10 for F), reflecting species ecological behaviour and preferences. For one given species, a low IV value indicates the species preference for low availability of the studied factor, e.g., light, water, or nitrogen. Several studies already focused on the Ellenberg IV validity at the scale of large ecological gradients (Ter Braak and Gremmen, 1987; Hawkes et al., 1997; Diekmann and Falkengren-Grerup, 1998; Schaffers and Sykora, 2000) and at the scale of a forest unit (Kirby and Thomas, 2000). In a study conducted in northeastern France, Thimonier et al. (1992) and Thimonier (1994) observed that N-Ellenberg IV was sensitive enough to reveal changes in soil eutrophication caused by aging of stands and deposition of atmospheric nitrogen.

Soil description was performed in 1999 from drill observations following a sampling frequency of one sample every two lines on the grid. For each sampled point, texture, thickness, and stone content of each soil horizon were observed. Depth to the groundwater table was recorded according to an assessment of oxydo-reduction spots in the clay layer. The parent material is sandstone, and soil type was intermediate between a luvisol and a stagnic luvisol according to the Food and Agriculture Organization (Granier et al., 2000a; 2000b). The humus at both stands was of the oligo-mull type. Three soil types were identified from field observations: dystric cambisol (DC), dystric cambisol stagnic (DCS), and luvisol stagnic (LVS). The main differences among types were the depth at which a silt–clay layer appears and the degree of wintery water excess, as revealed by oxydo-reduction spots. A

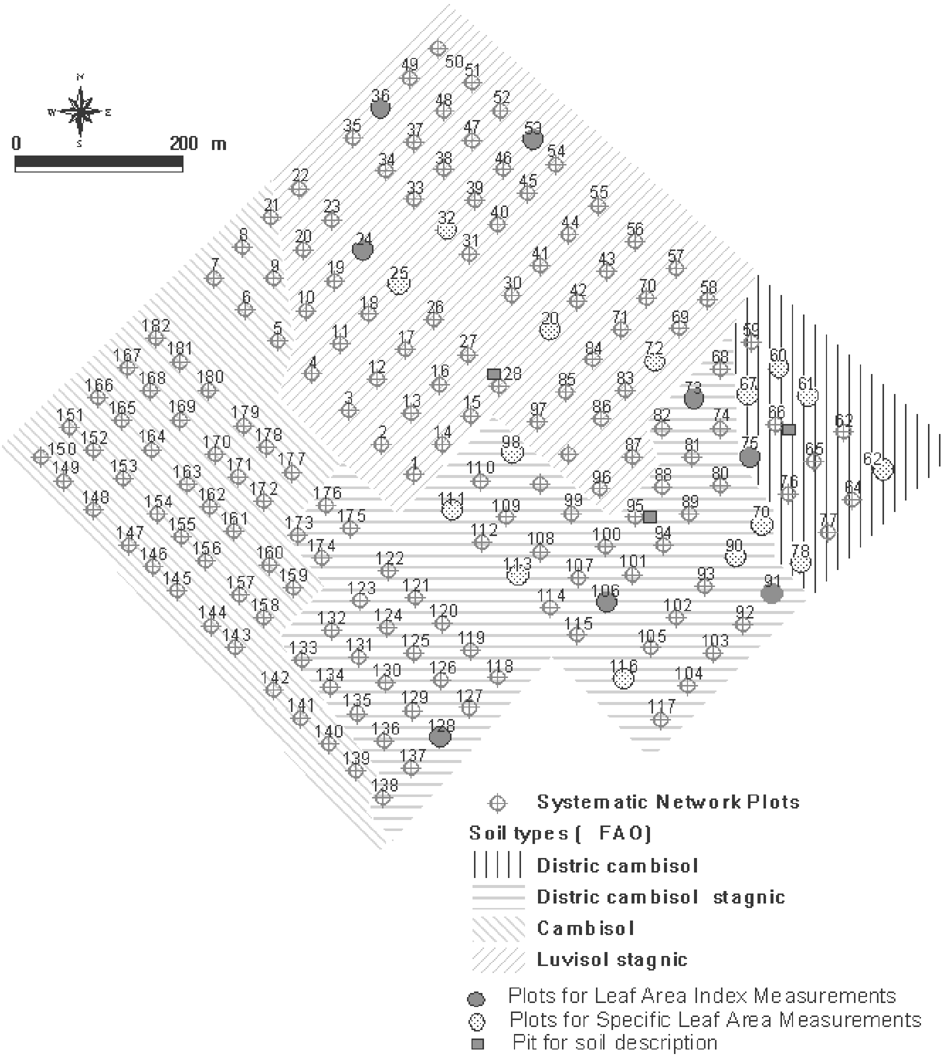

Figure 1. Systematic network plots and spatial position of the soil characteristics and locations of SLA and LAI estimation. Soil types according to the Food and Agriculture Organization (FAO).

complete description of the three soil types is given in Quentin et al. (2001).

Indirect plant area index measurements

Plant area index (PAI) and canopy openness (CO), defined as gap fractions averages over the whole hemisphere, were estimated using the LAI-2000 plant canopy analyser (LI-COR, Inc., Lincoln, Nebr.). Measurements were performed in mid-June of 2000 as maximum leaf expansion was achieved. Two intercalibrated sensors were used, one for below-canopy transmittance measurements, and the other at the top of a 22 m high scaffolding tower set up in the middle of the stands for the above-canopy incident diffuse radiation measurements. The two acquisitions were synchronized between the two operators using walkie-talkies. A view cap of 180° was adapted on both sensors to mask the operator, and two measurements were performed on each plot, in the east and west directions. To avoid direct sunlight, measurements were performed at sunset and sunrise. PAI values were calculated with C2000 software (LI-COR, Inc.) using the three upper rings of each sensor. According to Fassnacht et al. (1994), Dufrêne and Bréda (1995), and Planchais and Pontailler (1999), PAI values estimated using the three upper rings of the LI-COR, Inc. sensor were close to those obtained using direct techniques such as litter collection or allometry.

SLA measurements

A subsample of 23 plots was stratified from the grid according to soil types and PAI (LI-COR, Inc.) spatial variability to test both soil properties and canopy structure effects on litter SLA. These plots are representative of the variability that may be encountered on the 45 ha of the two stand units (see **Table 1** for more details). The plots chosen are mainly located in the two young beech stands (P217 and P218). Measurements were also made in one plot located in an older stand (P221) close to P217 from the point of view of dendrometrical and soil conditions (45 years old, density 4500 stems$\cdot$ha^{-1}, total basal area 28 m$^2\cdot$ha^{-1}).

To take into account possible temporal variability of SLA during the fall, leaf litter was collected three times (biweekly), on days of the year (DOY) 291, 304, and 325, from November to December. Leaf litter was collected within self-made square-shaped (0.5 m^2) traps. The bottom of the trap is self-draining, thus avoiding leaf decomposition. For each date and trap, a subsample of 30 leaves was randomly selected for SLA measurement. Leaf area was measured with the help of a leaf area meter (Licor 3000, LI-COR, Inc.) with a conveyor system (Licor 3050, LI-COR, Inc.). Individual leaf area, length, and width were recorded. The sampled leaves were then dried at 60°C to a constant weight (2 days) and weighed at the nearest 0.001 g.

Direct LAI estimates from litter collection

To properly measure leaf litter biomass, eight of the 23 plots were equipped with four additional traps located in the four cardinal directions, 4 m far from the plot centre. These eight plots were used to evaluate the impact of the SLA spatial variability on LAI calculation from litter collection. These eight plots for litter biomass monitoring were selected to screen the maximum variability of stem density and PAI found within the 23 plots and included all three soil types identified (**Table 1**). The subsample of leaves selected for SLA measurement was collected exclusively from the central trap for consistency of sampling among the 23 plots. Leaves collected in the four other traps were conditioned for dry mass measurements as detailed previously.

Testing the impact of the observed SLA variability on the LAI estimation

To test if the spatial variability of SLA has a significant effect on LAI calculation from litter fall, LAI estimations were implemented on the eight plots equipped with five traps according to four procedures. These procedures differ in the SLA employed to convert leaf biomass to leaf area. For the first procedure, the litter collected and dried at one date is converted using the date- and plot-specific SLA. This is the most accurate procedure and is referred to as 1-exact LAI (procedure 1). We then tested the impact of the temporal variability negligence by converting the total dry mass of litter collected during the three dates with the plot-specific SLA averaged over the three dates (referred to as 2-time neglected, or procedure 2). The between-plot variability was tested by converting the litter collected time by time (date per date) with date-specific SLA averaged over the eight plots: we used the same SLA for every plot, calculated

Table 1. Characteristics of beech litter leaves during the fall.

	SLA (cm^2/g)				Avg. leaf area (cm^2)	Avg. leaf weight (mg)
	DOY 291	DOY 304	DOY 325	Avg.		
Mean	230a	209a	253b	232	23.00	101.00
Min.	153	155	199	190	19.00	73.00
Max.	358	283	319	321	27.00	143.00
SE	12	6	5	6	0.50	3.00
CV (%)	24.00	14.80	9.80	12.40	10.30	20.50
No. of plots	23	23	22	68	68	68
No. of leaves	2070	2070	1980	6120	6120	6120

Note: Means followed by a different letter are significantly different at $p = 0.05$ according to the Tukey test. CV, coefficient of variation; SE, standard error.

at each date (referred to as 3-plot neglected, or procedure 3). Lastly, the coarse LAI (referred to as 4-coarse, or procedure 4) was calculated by averaging the SLA over both dates and plots.

Statistical analysis

Statistical analyses were conducted using SAS software (SAS Institute Inc., 1988). Assessment of spatial variability of SLA and morphological leaf characteristics was based on the coefficient of variation statistic as a normalized measure of the relative dispersion of each variable. General linear model ANOVA (Proc GLM of SAS software) was used to examine mean differences and interactions between leaf characteristics or Ellenberg IV and soil types. Means grouping was realised using the Tukey test, with significant differences at $p = 0.05$. The degree of correlation between leaves and soil or stand characteristics was assessed using Pearson's coefficient of correlation (r). The level of statistical significance was determined for a two-tailed P-value level of 5%. A stepwise regression (Proc reg of SAS software) was fitted to the 23 plots between soil and leaf characteristics to evaluate sources of SLA between-plot variability.

Results

Temporal and spatial variability of SLA

Descriptive statistics of SLA measurements and the average characteristics of leaf size and weight for each of the three collection dates are given in **Table 1**. SLA was on average 230 ± 11, 209 ± 6, and 253 ± 5 $cm^2 \cdot g^{-1}$ (±1 standard error) for DOY 291, 304, and 325, respectively (18 Oct., 31 Oct., and 21 Nov.). For the three dates, average SLA was 232 ± 3 $cm^2 \cdot g^{-1}$. Multiple comparison of means (according to the Tukey test at a significance level of 0.05) shows that the SLA measured on DOY 291 was significantly lower ($P = 0.0021$) than that measured on DOY 325. In our site, the period of leaf fall for beech ranges from mid-September to the end of November.

Spatial variability of SLA was quantified at each collection date as the coefficient of variation calculated among the 23 plots. Coefficients of variation were 24.0, 14.8, and 9.8% on DOY 291, 304, and 325, respectively. On average over the three dates, the coefficient of variation was 12.4%, which is quite high considering the spatial observation scale. The maximum of between-plot variability occurred during the first collection date, where 32% of the total amount of litter was obtained.

In the following we attempt to explain this spatial variability, according to canopy structure and soil properties. As the plot locations were chosen according to a PAI gradient that was as large as possible, the PAI ranged from 2.9 to 8.1, as shown in **Table 2** and **Figure 2**. No significant influences of PAI (r =

Table 2. Characteristics of plots chosen for SLA and LAI estimations, including soil type, plant area index (PAI), and litter specific leaf area (SLA) averaged among the three collection dates.

Plot No.	Soil type*	PAI ($m^2 \cdot m^{-2}$)	SLA ($cm^2 \cdot g^{-1}$)	Thinned†	No. of traps	Measurements on litter
72	LVS	4.64	219	Yes	1	SLA
25	LVS	5.98	188	No	1	SLA
35	LVS	6.73	211	No	5	SLA, LAI
29	LVS	6.91	207	No	1	SLA
53	LVS	7.52	291	No	5	SLA, LAI
32	LVS	7.79	210	No	1	SLA
24	LVS	7.89	210	No	5	SLA, LAI
91	DC	2.88	211	Yes	5	SLA, LAI
78	DC	4.24	186	Yes	1	SLA
75	DC	4.67	275	Yes	5	SLA, LAI
63	DC	4.72	264	Yes	1	SLA
60	DC	4.89	229	Yes	1	SLA
61	DC	5.50	216	Yes	1	SLA
79	DC	6.47	214	No	1	SLA
106	DCS	4.54	218	Yes	1	SLA
67	DCS	4.55	228	Yes	1	SLA
73	DCS	4.72	259	Yes	5	SLA, LAI
111	DCS	5.49	222	Yes	1	SLA
98	DCS	5.66	210	Yes	1	SLA
128	DCS	5.66	230	No	5	SLA, LAI
116	DCS	6.60	321	Yes	5	SLA, LAI
90	DCS	7.63	272	No	1	SLA
113	DCS	8.09	238	No	1	SLA

*DC, dystric cambisol; DCS, dystric cambisol stagnic; LVS, luvisol stagnic.

†Indicates if sampled stands were thinned in 1999 or not.

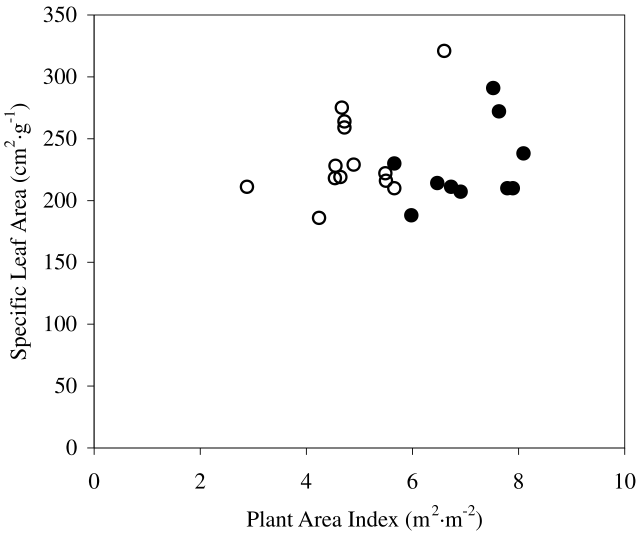

Figure 2. Specific leaf area variation of litter leaves versus plant area index as measured by the LAI-2000. Solid symbols are for control plots, and open symbols for thinned plots. The correlation between the two variables is not significant (r = 0.297).

0.297) or canopy openness (CO) (r = –0.19) were observed on SLA. PAI and CO did not correlate with average leaf area (r = –0.23 and 0.185, respectively) or leaf weight (r = –0.28 and 0.237, respectively) (**Figure 2**). The plots were gathered in a second step in two groups: thinned (from P217) and unthinned (from P218). No significant difference was pointed out between these two groups for SLA (ANOVA: F(1,21) = 0.12, P = 0.72) or leaf weight and leaf area (P = 0.19 and 0.27, respectively). These results indicate that the morphological characteristics of leaf litter are not influenced by canopy structure, even after a thinning.

Relations with soil properties

The soil properties of the 23 studied plots, related to water and nitrogen, and Ellenberg's indicator values averaged by soil types are presented in the **Table 3**. The soil chemical analyses indicate differences in nitrogen content, which is in agreement with the estimated N-Ellenberg IV, which is significantly different for the three soil types (P = 0.0164). According to hydric properties, the three soils exhibited different extractable water content as calculated from soil texture (P = 0.0116) and different depth of appearance of hydromorphy spots (P = 0.0001). The F-Ellenberg IV, reflecting soil moisture, also differs among the three groups of plots (P = 0.0117) but is not related to depth of hydromorphy or soil extractable water. Its significance in these site conditions is then redundant with the N-Ellenberg IV, as both are highly correlated (correlation coefficient = 0.44). We can then consider that the three groups of plots, according to their soil properties, are discriminated according to both water and nitrogen fertility. The next question is to test if the fertility can explain the differences in litter SLA. According to the average values per soil type, SLA decreases when N-Ellenberg IV increases (i.e., when N availability increases) (ANOVA: F(2,20) = 2.634, P = 0.0965). The decrease in SLA may be attributed to the decrease of individual leaf area, as this parameter is significantly different among soil types (P = 0.0196). Leaf area was then driving part of the spatial variability of SLA, and leaf dry weight (resulting from both leaf thickness and leaf density) was varying according to a random spatial pattern (P = 0.7074).

The most complete model suitable to explain the variance in SLA among the 23 studied plots involves a negative effect of N-Ellenberg IV (explaining 18.6% of total variance), a positive effect of plot PAI (12.0%) and individual leaf area (12.1%), and a negative effect of soil extractable water (10.2%) (**Table 4**). Only 52.9% of total variance is explained in this way, so the residual error term is high. One may hypothesize that either other site factors and climatic conditions are involved or the remaining variance is due to a random effect. In any case, numerous factors are responsible for SLA spatial variability, with nitrogen and canopy leaf area index being the most significant.

Impact of the observed SLA variability on the LAI estimation

LAI was calculated according to the four procedures described previously: the reference LAI, a procedure neglecting variability between collection dates, a procedure neglecting plot variability, and a rough estimation. These four procedures led to quite different LAI values (**Figure 3**; **Table 5**). The differences between exact and approximate

Table 3. Comparison among the three plot groups (i.e., soil types) of SLA, soil nitrogen content, acidity, water regime, and light regime.

		Nitrogen			Acidity		Water regime			Understory light regime	
	SLA (cm^2/g)	C:N	N ($mg \cdot g^{-1}$)	N-Ellenberg IV	pH	R-Ellenberg IV	SEW (mm)	DWT (cm)	F-Ellenberg IV	PAI ($m^2 \cdot m^{-2}$)	L-Ellenberg IV
LVS (n = 8)	216	12.8	1.97	3.7	5.1	3.6	156	54	4.5	6.5	4.6
DC (n = 6)	232	13.3	1.95	3.5	4.8	3.2	101	78	4.4	4.8	4.4
DCS (n = 9)	246	14.9	1.61	3.4	4.9	3.4	149	69	4.3	5.9	4.3
F(2,20)	2.67			5.09		2.14	5.62	21.50	5.61	2.60	3.59
$P > t$	0.070			0.0164		0.144	0.0116	0.0001	0.012	0.099	0.047

Note: Ellenberg IV (F, available water; L, understory light; N, nitrogen; R, acidity) values are calculated from soil vegetation on each plot and averaged by group. Pedological data presented concern the organic layer and come from pith observations (C:N, N, pH, one analysis per pith and type of soil). Soil extractable water (SEW) and depth of water table (DWT) are averaged values from observations on each plot. PAI is calculated from LI-COR, Inc. LAI-2000 measurements on each plot and averaged by group.

Table 4. Regression of SLA on the N-Ellenberg index, PAI, individual leaf area (iLA), and soil extractable water (SEW).

	Coefficient	SE	Standard coefficient	F value	Adjusted R^2	Partial R^2
Intercept	205.096					
N-Ellenberg IV	–43.762	18.814	–0.366	5.410	18.6	18.6
PAI	14.016	3.704	0.686	14.320	30.6	12.0
iLA	6.141	1.993	0.507	9.498	42.7	12.1
SEW	–0.298	0.132	–0.407	5.092	52.9	10.2

Table 5. Statistics on differences between different LAI calculation procedures 1–4 from litter biomass performed on eight plots.

Difference	Mean	Min.	Max.
1 vs. 2	0.27 (5)	0.07	0.54 (8)
1 vs. 3	0.52 (9)	0.01	1.61 (24)
1 vs. 4	0.59 (7)	0.02	1.03 (16)

Note: 1, exact calculation, taking into account both time- and plot-specific SLA; 2, time neglected, with only time variability of SLA neglected and plot variability taken into account; 3, plot neglected, with plot variability of SLA neglected and variability among time collections taken into account; 4, coarse, with both time and plot variability of SLA neglected. Percentages are given in parentheses.

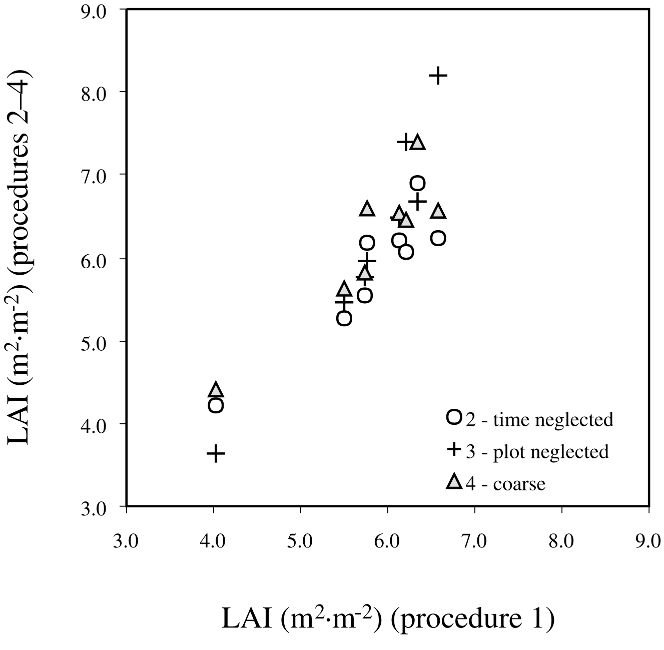

Figure 3. Scatter plot of plot LAI calculations based on varying SLA estimations (procedures 2 to 4) versus LAI estimated from plot- and time-specific SLA estimates (procedure 1).

procedures ranged from 1 to 24%; every approximate procedure leads to an overestimation of LAI (**Figure 3**). The differences in LAI estimations also increased with an increase in the LAI value, as a result of multiplying SLA differences by largest collected litter biomass. We note that the between-plot variability has a greater consequence than variability between collection dates, leading to serious errors that may overcome the sensitivity levels of some water-balance processes. LAI estimation errors in our example would reach 7–24% at one plot estimation while using the mean SLA value for all plots (procedure 3 or 4), but LAI averaged among plots was not significantly different between calculations (**Table 6**). If we had used a single SLA value measured at one location for all eight plots, however, we would have found an average LAI value significantly different from estimations using plot-specific SLA in three cases out of eight (**Table 6**).

Discussion

The average SLA we measured in this study (232 $cm^2 \cdot g^{-1}$) is in the same order of magnitude as estimates given by Vanseveren and Herbauts (1977) in different Belgium–Lorraine beech stands, the value 256 $cm^2 \cdot g^{-1}$ reported by Chason et al. (1991) in an American mixedwood stand, and the value 242 $cm^2 \cdot g^{-1}$ measured by Hochbichler (1997) in beech stands in the Vienna area.

Although our study site has a small spatial extent (45 ha), a large range of SLA values was observed (191–267 $cm^2 \cdot g^{-1}$).

Table 6. Average LAI values (calculated over the eight sampling plots) using different SLA values measured at one plot only or using four procedures.

SLA provenance taken from plot	SLA value used ($cm^2 \cdot g^{-1}$)	Average LAI ($m^2 \cdot m^{-2}$)
53	291, constant	7.72a
75	267, constant	7.08b
73	230, constant	6.20c
Time specific (procedure 3)	230, 209, 253	6.18c
Coarse (procedure 4)	233, constant	6.10c
128	230, constant	6.10c
106	226, constant	5.99cd
Plot specific (procedure 2)	Variable among plots	5.83cd
Exact (procedure 1)	Variable among plots	5.79cd
35	211, constant	5.60d
24	210, constant	5.57d
91	191, constant	5.07e

Note: Procedure 1, SLA measured at each time and plot; procedure 2, SLA plot specific, with time neglected; procedure 3, SLA time specific, with plot variability neglected; procedure 4, average value over time and plots. LAI values followed by the same letter are not significantly different at $P < 0.05$ according to the Tukey test.

This result is consistent with observations from ecologically contrasted forests (166–200 $cm^2 \cdot g^{-1}$ in three different aspen stands of low soil fertility; Jurik et al., 1985). Mean leaf area contributed more to this variability than leaf weight, which appears to be more randomly distributed among dates and plots. Vanseveren and Herbauts (1977) have already pointed out a significant decrease in beech litter SLA with an increase in both the C:N ratio and the nitrification index along an ecological gradient. Our results on leaf litter are also in agreement with results found on green leaves. Minotta and Panzauti (1996) and Heath and Kerstiens (1997) reported that beech seedlings grown with a high nutrient supply had considerably lower leaf area to tree dry mass ratios and lower SLA under both ambient and elevated CO_2. Coyne and van Cleve (1977) also observed a decrease in SLA with an increase in fertilization in aspen stands. Little is known about mechanisms leading to the interactions between SLA and nutrient conditions for forest trees. Moreover, the complexity of such mechanisms is reflected by the fact that opposite effects of nutrient availability on SLA have already been reported (e.g., Jose and Gillespie, 1997; Jurik, 1986; Garnier and Freijsen, 1994). The main effect we found was that the decrease in individual leaf area (leaf size) was even greater than the decrease in SLA. It is conceivable that large leaf nitrogen content per unit mass, as a result of good nutrient availability, permits a decrease of leaf size. The resulting nitrogen content per unit area, which was proved to be a key parameter for photosynthesis, would then be conserved with a lower carbon investment in leaves. In contrast, SLA was not found to react to fluctuations in soil water regimes in our study, probably because soil extractable water was quite high in all plots. Another study along a precipitation gradient has already noted the low influence of water availability on leaf parameters, including SLA, of a deciduous species, *Quercus faginea* (Castro-Diez et al., 1997). By contrast, Kubiske and Abrams (1992) reported a higher SLA in *Quercus rubra* L. seedlings from a xeric site than from a mesic site.

The influence of light environment on green leaf characteristics within the canopy is well known (Goulet and Bellefleur, 1986; Niinemets and Kull, 1994). Light microclimate influences the geometrical and optical properties of leaves and determines the proportions of sunlit and shaded leaves within the canopy. Beech presents a strong leaf differentiation between these two leaf categories that is reflected by both leaf thickness and SLA (Aussenac and Ducrey, 1977; Bartelink, 1997). As the pattern of leaf differentiation follows the light extinction profile, the amount of so-called sunlit leaves is limited to the upper parts of the canopy. One could therefore expect a relationship between LAI and litter SLA that would reflect the average SLA profile: a high LAI value would involve a great amount of shaded leaves and then decrease the mean SLA value. The fact that we did not find such a relationship can be explained by the consequences of thinning on the extinction profile, but no significant relationship was found, even within unthinned plots. This could be due to a high within-habitat variance of SLA, especially for beech, which is a shade-tolerant species. The variance was even higher than that reported for green leaves (Knapp and Carter, 1998). Moreover, litter leaves are dissimilar from green leaves, being transformed by element migration that occurs before they fall down, and continuing with lessiviation and decomposition when the leaf stays in the trap. These two processes may introduce some random noise, hiding a relationship, even if leaf lessiviation is minimized by low temperature and short residence time within the traps (2 weeks maximum). We cannot assess here if site fertility and canopy leaf area influence mainly litter properties, or if a similar pattern of SLA spatial variability would be observed on green leaves during the season. Complementary investigations are needed to answer this question. Jurik et al. (1985) noted that SLA of high-light leaves sampled just before leaf fall in October was approximately 30% lower than that of leaves during most of the year. Estimates of LAI derived from litter traps are highly dependent on the ratio of leaf area to leaf mass, as reported by Jurik et al., who noted that the greatest uncertainty in the litter fall method is probably the relationship of litter weight to leaf area. The most likely error is an overestimation of SLA owing to leaf decomposition. This is the reason why the frequency of litter collection is crucial, and likewise traps with good drainage are recommended rather than collection next to the soil. Our results underline another source of variation in the ratio of litter weight to leaf area, that is the within-stand spatial variability. One may suggest determination of SLA in each location where litter biomass is collected, i.e., sample leaves for SLA measurement from all the traps.

Our results illustrate the successful application of understory vegetation in assessing site quality at a within-forest unit scale. The below-canopy light gradient we observed from understory vegetation resulted from variability in local canopy PAI, leading to L-Ellenberg IV values ranging from 4.0 to 5.2. A similar range was reported in a study including 6285 beech forest plots in Nordic countries (Diekmann et al., 1999). The light gradient we described within a stand was comparable to that reported at a regional scale. Concerning the variability of site fertility, the nutrient regime reflected by the N-Ellenberg IV was consistent with soil chemical analysis and suitable to quantify spatial variability in nitrogen supply on this scale. Hawkes et al. (1997) already reported a strong correlation between soil data and both R (acidity) and N (nitrogen) Ellenberg indices. The N-Ellenberg IV values were quite variable between plots; a similar range was observed in forest (Thimonier, 1994) or regional (Badeau, 1995) scales in beech stands in northeastern France. Hawkes et al. also indicated ranges of two units of N-Ellenberg IV among plots within a mixed stand of larch, beech, and sycamore. Nevertheless, variability in the soil moisture regime in our study area was better quantified by soil observation than with F-Ellenberg IV. This lack of soil vegetation performance for soil moisture assessment could partly be due to the fact that fewer species have been assigned F-Ellenberg values as compared with N or R. A similar conclusion was also reported in a wider range of soil moisture regimes (Hawkes et al., 1997) and a limited variability on F-Ellenberg IV, restricted to less than 1 unit (4.8–

5.7), in the beech communities from the previously mentioned meta-analysis in Nordic countries (Diekmann et al., 1999).

Conclusions

Even within a small experimental study area, commonly considered as homogeneous, litter SLA showed spatial variability as great as that encountered at a regional scale. The results also showed to what extent litter SLA influences the estimation of LAI. This between-plots variability in SLA was mainly explained by leaf area, which was found to be sensitive to soil properties, especially nitrogen and water content. The influence of environmental conditions on SLA should be investigated to understand the processes and causes of the relation linking leaf parameters with soil properties, not only on litter leaves but also on green leaves.

Our results clearly showed that the between-plot SLA differences were large enough to generate bias in the calculated values of LAI, even working within a small area, i.e., within a forest stand. This implies that SLA should not be estimated only in one particular location and then applied elsewhere to convert litter fall biomass to leaf area per ground unit area. Therefore, the SLA ratio should be determined at each location where traps are used to monitor litter biomass, to take into account the spatial variability of the SAL ratio. The determination of SLA requires the measurement of individual leaf area, which by itself represents important ecophysiological data that allow determining if LAI variability results from a change in the number or size of leaves. The fact that variability in soil conditions influences SLA emphasizes the necessity of site-specific measurements for both litter biomass and SLA for studies at larger scales. A previous exploratory analysis of fertility conditions may be quite useful, for example, based on the understory species composition and its bio-indicator ability of site fertility. On the other hand, temporal variations in SLA during the fall did not significantly influence the LAI estimate and may therefore be omitted. Nevertheless, even if SLA could be determined once during the fall, we recommend that the litter be collected, dried, and weighed more frequently to avoid litter decomposition and mass loss. Lastly, interannual variations in SLA may also be large enough to be accounted for in LAI estimations. A study conducted by Bussotti et al. (2000) on the green leaves of beech trees revealed variations in the SLA value of up to twofold about the average value. Drought effects were responsible for the variability in the study by Bussotti et al., but seed production and defoliation have also been proven to dramatically decrease litter SLA as a result of modification of the allocation of tree carbon (Burton et al., 1991).

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