



# Estimating leaf area index of mature temperate forests using regressions on site and vegetation data

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## ABSTRACT

Canopy gap fraction and leaf area index (LAI) were measured using hemispherical photography in 91 mature forests across Switzerland, including coniferous, broadleaved and mixed stands. The gap fraction and LAI derived from five photographs per site could be reproduced with a high coefficient of determination ( $R^2 > 0.7$ ) by regression against simple stand parameters obtained from vegetation surveys: coverages of the tree, shrub and herb layers, and tree height. The method appeared to be robust across the different types of forests. Applied to 981 sites across Switzerland, the regression model produced LAI values ranging from 1.4 to 6.7. These predictions were compared with site variables not included in the regression. LAI appeared limited by the altitude, with maximal values decreasing by one third from 400 to 2000 m above sea level. Water availability was also clearly a limitation at sites with a negative water balance, i.e. where the yearly potential evapotranspiration exceeded the precipitation. High or low values of a humidity index based on the ground vegetation also corresponded to a limitation of the LAI, with shorter trees at dry sites and more open canopies at wet sites. Compared to optical measurements (including hemispherical photography), our regression method is fast and inexpensive. Such an approach appears very promising for obtaining reliable estimates of LAI for many sites with low costs. These estimates can then be fed into process models at the stand level.

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## 1. Introduction

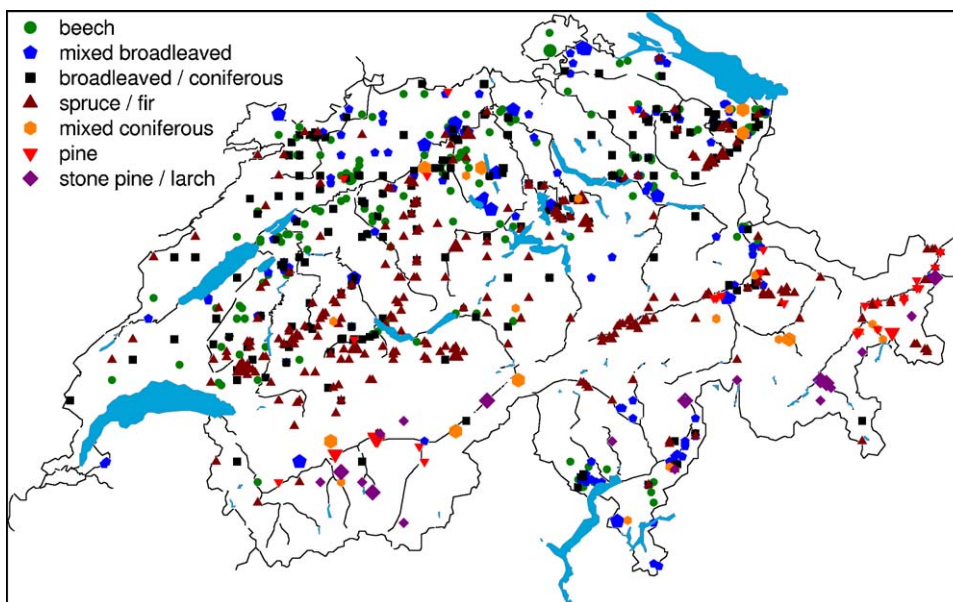
Leaf area index (LAI), defined as one half the total leaf area per unit ground surface area (Chen and Black, 1991), is an essential canopy characteristic that controls the energy, water and carbon fluxes between the terrestrial ecosystems and the atmosphere (Bonan, 1993). Most ecosystem process models that simulate carbon and water cycles on a stand or regional scale thus require LAI as an input variable (e.g. Running and Coughlan, 1988; Running and Gower, 1991). LAI can be directly obtained by sampling vegetation destructively, determining the dry mass of the whole foliage and, on a subsample of the harvested foliage, the specific leaf area (SLA, the ratio of fresh leaf area to dry foliage mass). In forests, destructive harvesting is commonly associated with the development of allometric relationships between LAI and variables such as tree stem diameter or sapwood cross-sectional area (e.g. Long and Smith, 1988; Gower et al., 1997). Such allometric equations are species and site-specific. Applying these equations to other sites may result in substantial errors (Grier et al., 1984), since several factors influence allometric coefficients, in particular nutrient availability, water regime and tree age.

As an alternative to destructively harvesting foliage, the LAI of broadleaved stands can be determined semi-directly from litterfall sampling during leaf fall. LAI is then calculated by multiplying the collected mass of leaves by the specific leaf area, which must be determined for each tree species separately. The SLA should also be determined specifically for the studied site, since it can vary with site fertility, within and between years, or with the duration of the collection interval (Bréda, 2003).

Because both the direct and the semi-direct methods for determining LAI are labour intensive and time consuming for forest canopies, a number of techniques relying on the radiative transfer theory (Anderson, 1971; Ross, 1981) have been developed to derive LAI from measurements of the transmission of radiation through the canopy. The most widely applied indirect techniques infer LAI from the distribution of the gap fraction (i.e. the fraction of the view in some direction from beneath the canopy that is not blocked by foliage). In these techniques, LAI is obtained by the inversion of the model describing the attenuation of radiation through the canopy, using gap fraction data measured over a range of zenith angles. Several instruments and methods, which include the hemispherical photography technique, are available to measure the distribution of the gap fraction (see review by Bréda, 2003).

The hemispherical photography technique derives gap fraction data from photographs of the canopy taken upward with an extreme wide-angle lens (typically 180° viewing angle). This tech-

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**Fig. 1.** Map of Switzerland showing the location of the 91 sites where the gap fraction and LAI were assessed with hemispherical photography (large symbols) and the 981 sites to which the regressions obtained were applied (small symbols). See Table 1 for the definition of the forest types.

nique requires great care at several steps of the data acquisition, in particular when selecting the exposure settings in the field, or when choosing the threshold to distinguish the canopy from the sky during image analysis (Thimonier et al., 2010). However, compared with sensors that measure light transmission, it has the major asset that it permanently archives the canopy structure. Moreover, using the information available from the photographs, the effects of a ground slope or of canopy clumping on LAI estimation can be directly corrected for. Hemispherical photography, like all methods based on the measurement of light transmission and gap fraction, is affected by the ambient light conditions, especially by the presence of the sun and of clouds. This considerably limits their use across sites in large-scale studies.

Methods of estimating LAI by remote sensing have been developed which rely on the different reflectance properties of vegetation and soil (Weiss and Baret, 1999). In the case of forests, deriving LAI from satellite imaging faces several challenges, among them the difficulty of separating the tree canopy from the ground vegetation, the need to account for canopy clumping, and the effect of ground slopes. Until recently, the forest LAI datasets obtained from remote sensing were, therefore, not satisfactory and limited in their range (e.g. Rautiainen, 2005; Garrigues et al., 2008). In recent years, there has been significant progress, especially using multi-angular sensors. Analysing the reflectance at different angles relative to the nadir and to the sun indeed provides information on the 3-dimensional structure of forest canopies (Hasegawa et al., 2010; Pisek et al., 2010). Corresponding datasets are being developed but their resolution is still limited to the kilometre scale and they need to be validated more broadly by comparison with ground-based measurements.

In this study, we estimated the LAI of mature forest stands using digital hemispherical photography at some 100 sites distributed across the whole of Switzerland. Our aim was to evaluate whether LAI could be alternatively derived from vegetation surveys, which are commonly carried out on forest sites. Our final objective was to obtain the LAI values needed as input data to run a water balance model (CoupModel; Jansson and Karlberg, 2004) on over a thousand forest sites across Switzerland for which vegetation data are available along with geophysical and soil data. We also wanted, at the same time, to examine how LAI relates to environmental factors.

## 2. Materials and methods

### 2.1. Field campaign

Hemispherical photographs of the canopy were taken in the summers 2004–2008 at 114 forest sites distributed across all the main regions of Switzerland (Jura, Plateau, Northern Pre-Alps, Alps, and Southern Alps; Fig. 1). These sites have also been used in other studies conducted by researchers at our institute (WSL, Birmensdorf). Vegetation surveys were carried out at these sites. All plant species occurring in a square 200-m<sup>2</sup> plot in the herb, shrub and tree layers were recorded using the Braun-Blanquet cover abundance scale (Braun-Blanquet, 1964; Mueller-Dombois and Ellenberg, 1974). This method is fast and generally recognised as sufficiently accurate to assess the prevailing environmental conditions and how they change (Wikum and Shanholtzer, 1978). It has been widely used in many countries on all five continents with, for example, more than 6000 forested sites assessed in Switzerland (Wohlgemuth, 1992) and in France (Gégout et al., 2005). As part of the vegetation survey, the coverage of the tree, the shrub and the herb layers were estimated visually as the proportion of their vertically projected area. Tree height was measured with a Vertex III ultrasonic instrument (Haglöf, Långsele, Sweden) on at least two of the tallest trees. The height of the shrub layer was estimated by the observers.

At each site, five hemispherical photographs of the canopy were taken, one at the centre of the vegetation plot and four in the corners. An exception was the data set stemming from the seven LWF (Long term Forest Ecosystem Research) sites. At the LWF sites, photographs were taken at 16 locations systematically distributed over a 43 m × 43 m area (Thimonier et al., 2010). Photographs were taken 1.5 m above ground using a digital camera (Coolpix 4500, Nikon, Tokyo, Japan) with a 183° fish-eye lens (Nikon FC-E8) fitted to a plate with a bubble level and compass, and mounted on a tripod. From each of the five points per plot, four photographs were taken with different exposures. The first was in automatic mode. The exposure of the second was set manually, with the aperture fixed at F/5.3, and the shutter speed set according to the reading of a spot-meter (Asahi Pentax V, Asahi, Tokyo) pointed towards a canopy gap near the zenith. The third and fourth photographs were then taken with the exposure increased

**Table 1**

Forest types defined for this study and their proportions among the sites with hemispherical photographs (n/91) and among those used for the model application (n/981).

Forest type	Species	n/91	n/981
Beech forests	<i>Fagus sylvatica</i> ≥ 50% Broadleaved species > 75%	6	231
Mixed broadleaved forests	Broadleaved species > 75% <i>Fagus sylvatica</i> < 50%	17	137
Mixed broadleaved/coniferous forest	Broadleaved and coniferous species, both between 25 and 75%	36	203
Spruce/fir forests	<i>Picea abies</i> and/or <i>Abies alba</i> ≥ 50% Broadleaved species < 25%	12	342
Mixed coniferous forests	Coniferous species ≥ 75% ( <i>Picea abies</i> + <i>Abies alba</i> ), <i>Pinus sylvestris</i> and ( <i>Pinus cembra</i> + <i>Larix decidua</i> ) all < 50%	8	18
Pine forests	<i>Pinus sylvestris</i> and/or <i>Pinus mugo</i> var. <i>arbores</i> ≥ 50% Broadleaved species < 25%	5	35
Stone pine/larch forests	<i>Pinus cembra</i> and/or <i>Larix decidua</i> ≥ 50% Broadleaved species < 25%	7	15

by one stop and two stops, respectively, by decreasing the shutter speed.

## 2.2. Processing of the hemispherical photographs

For each point, the picture chosen for further processing was the one with the highest exposure but without noteworthy blooming effects. Blooming, as described by Leblanc et al. (2005) and Thimonier et al. (2010), occurs when the camera sensor becomes light saturated, producing overly large white patches. Picture selection was thus aimed at optimising the contrast between the vegetation and the sky, while avoiding the disappearance of vegetation elements along the borders of bright gaps. The selected hemispherical photographs were then processed using the Hemisfer software, developed at the WSL research institute (Schleppi et al., 2007). A zenith angle of 75°, divided into five concentric rings of 15°, was used to analyse the photographs. Only the blue colour channel was used in order to improve the contrast between the sky patches and the vegetation. The threshold to separate them was calculated according to the automatic procedure of Nobis and Hunziker (2005) implemented in Hemisfer, taking the gamma value ( $\gamma = 2.2$ ) of the picture into account (Thimonier et al., 2010).

The analysis of the pictures was based on the model of an ellipsoidal leaf angle distribution (Campbell, 1986). Campbell's equations were solved by minimizing the sum of squared errors between the measured and the predicted contact frequencies and by weighting each ring with its solid angle (Schleppi et al., 2007; Thimonier et al., 2010, including formulae in appendix). The following variables were calculated: (1) the effective LAI, i.e. the LAI under the assumption of a random foliage distribution ( $L_e$ ) and the corresponding leaf angle ( $\alpha_e$ ); (2) the canopy openness (gap fraction) in a vertical direction ( $T$ ) resulting from  $L_e$  and  $\alpha_e$ ; (3) the corrected LAI ( $L_c$ ) and leaf angle ( $\alpha_c$ ) obtained using the gap separation method of Chen and Cihlar (1995) (correction of canopy clumping) and (4) the fraction of large canopy gaps in a vertical direction ( $G$ ) resulting from this gap separation. In all cases, the effect of the ground slope was taken into account using the procedure developed by Schleppi et al. (2007). All photographs were analysed as a batch with Hemisfer, which allowed the LAI and leaf angle values to be calculated not only per photograph but also per site.

The leaf angles obtained from the computation with Hemisfer were used as criteria for site selection. The sites were the calculated leaf angles were either smaller than 25° or greater than 75° were discarded as such angles are very unlikely. They indicate too many irregularities within or between photographs, in which case more than five photographs would have been necessary to characterise the site. This criterion excluded 16 sites. Other reasons for

excluding sites were: because a forest edge was close, i.e. within the analysed circle on the pictures (six sites), or because the forest stand consisted of young trees (one site). In the end, 91 sites (all mature stands) were kept for the statistical analysis.

Among the analysed sites, we further chose two subsets of 10 sites each, one with the smallest trees and one with the tallest trees. For each of these 20 sites, we chose one photograph with the LAI and leaf angle close to the site average to examine the effect of the stems visible on the photographs. We excluded the large stems on the photographs by painting them in red, then re-analysed the photographs with the option of excluding this red colour from the calculations.

## 2.3. Statistical models and predictors

The LAI and the related canopy variables for the 91 study sites were analysed as a function of independent variables using general linear models. The set of predictors consisted of four groups of variables: (1) geophysical site characteristics, (2) classifications of forest types and regions, (3) height and coverage of the vegetation layers and (4) ecological indicators based on the botanical composition. The primary geophysical site characteristics were geographical coordinates, altitude, slope, aspect and potential solar radiation. The annual potential solar radiation was calculated from the angle of the incidence of the sun determined in an astronomical model in 10-min time steps from the slope, aspect and latitude. A regression model was then developed to estimate the potential solar radiation directly from the slope, aspect and latitude, so that it can be calculated without having to run the astronomical model. We found the following relationship, which is valid for all sites across the country with a coefficient of determination  $R^2 = 0.996$ :

$$Q = 0.06312 + 0.19642 (\cos \Phi)^2 \cos \nu - 0.10629 \sin \nu \cos \varepsilon \sin 2\Phi - 0.02384 \cos \Phi \cos 2\Phi - 0.01174 \sin \nu \cos \Phi \cos 2\varepsilon \quad (1)$$

where  $Q$  is the fraction of the solar constant reaching the ground on average over the year (dimensionless),  $\Phi$  is the latitude,  $\nu$  the slope and  $\varepsilon$  the aspect (North = 0). Alternatively, we also used the south component  $s$  of the slope (also dimensionless) calculated as:

$$s = -\sin \nu \cos \varepsilon \quad (2)$$

Forest types were classified as indicated in Table 1. Alternatively to the forest type, we also tried using the proportion of broadleaved species in the tree stand. The height and coverage of the vegetation layers were determined as described above. The coverage values were used either directly or as transformed to a simple estimate of

**Table 2**  
General linear models of variables derived from hemispherical photography as functions of variables from vegetation surveys.

Dependent variable	Model	Regression formula	R <sup>2</sup>	SE	PE
Effective LAI	Optimal	$L_e = 0.76 - 0.60s + 0.051h_t + 0.57L_a - 0.04L_b$	0.71	0.78	0.83
	Simplified	$L_e = 0.95 + 0.044h_t + 0.58L_a - 0.05L_b$	0.70	0.79	0.83
LAI corrected for clumping	Optimal	$L_c = 1.44 + 0.048h_t + 0.51L_a - 0.05L_b$	0.70	0.74	0.77
Canopy openness (vertical gap fraction) (%)	Optimal (1)	$T = 90 - 0.54C_a + 0.08C_b - 13.1N_{\text{Landolt}}$	0.76	7.3	7.6
	Optimal (2)	$T = 51 - 0.67C_a + T_i$ Beech forests: $T_i = 16.4$ Mixed broadleaved forests: $T_i = 17.8$ Mixed broadleaved/coniferous forest: $T_i = 14.7$ Mixed coniferous forests: $T_i = 17.3$ Spruce/fir forests: $T_i = 15.4$ Pine forests: $T_i = 26.4$ Stone pine/larch forests: $T_i = 17.6$	0.75	7.6	8.3
	Simplified	$T = 70 - 0.70C_a$	0.71	7.8	8.0
Fraction of large canopy gaps (vertical projection) (%)	Optimal	$G = 69 - 0.45C_a + 0.07C_b - 10.2N_{\text{Landolt}}$	0.67	7.5	7.8
	Simplified	$G = 54 - 0.58C_a$	0.63	7.8	8.0

$s$  = south slope component (Eq. (2)),  $h_t$  = tree height (m),  $L_a$  = simple LAI estimate above 1.5 m (Eq. (4a)),  $L_b$  = simple LAI estimate below 1.5 m (Eq. (4b)),  $C_a$  = vegetation cover above 1.5 m (Eq. (5a)),  $C_b$  = vegetation cover below 1.5 m (Eq. (5b)),  $N_{\text{Landolt}}$  = Landolt's nutrients index,  $T_i$  = effect of the forest type on  $T$  (least square means), SE = standard error of the estimate (root of mean square error) and PE = prediction error (standard error for out-of-sample predictions).

a leaf area index:

$$L = -2 \ln(1 - C) \quad (3)$$

where  $L$  is the LAI directly calculated from the coverage  $C$  of a vegetation layer ( $0 \leq C \leq 1$ ). Without further information about foliage angles and canopy clumping, this formula gives an estimate based on the Beer–Lambert–Bouguer law of light absorption. It assumes a spatially randomly distributed foliage with tip angles following a spherical distribution (Campbell, 1986), which gives, on average, a projection coefficient of 0.5, and thus the reciprocal factor 2 in the equation.

As usual in forests, hemispherical photographs were taken below the tree layer and above the herb and moss layers, but partly above and partly below the shrub layer. They are therefore not directly comparable with the vegetation surveys. In order to make the stand variables comparable with the hemispherical photographs, we estimated the LAI of the shrubs below and above the height at which the photographs were taken (1.5 m). This was done by assuming a homogenous foliage density over the total height of the shrub layer. We then added the contribution of the high shrubs to the tree layer and that of the low shrubs to the herb layer (Eqs. (4a) and (4b)):

$$L_a = L_t + L_{hs} \quad (4a)$$

$$L_b = L_{ls} + L_h \quad (4b)$$

where  $L$  is the LAI, with indices indicating the following vegetation layers: a = above 1.5 m, t = tree layer, hs = high shrubs (>1.5 m), b = below 1.5 m, ls = low shrubs (<1.5 m), and h = herb layer. Finally, the coverage above and below the height of photography was calculated using Eqs. (5a) and (5b) (i.e. the reciprocal form of Eq. (3)):

$$C_a = 1 - e^{-L_a/2} \quad (5a)$$

$$C_b = 1 - e^{-L_b/2} \quad (5b)$$

The fourth group of variables tested as predictors were ecological indicators derived from the botanical surveys. Landolt's (1977) indicator values of the plant species were used to quantify the site ecological conditions regarding soil nutrient availability ( $N_{\text{Landolt}}$ ), soil acidity ( $R_{\text{Landolt}}$ ), light ( $L_{\text{Landolt}}$ ), temperature ( $T_{\text{Landolt}}$ ) and soil moisture ( $F_{\text{Landolt}}$ ). Each of these indices is defined on a scale between 1 (minimum) and 5 (maximum). Only the species recorded in the herb-layer, excluding the tree seedlings, were used to calculate average Landolt values. The relative abundance of the species

was not used as a weighting factor because this would have given too much weight to some species with vegetative reproduction, while rarer species with a narrow ecological niche would have received too low a weighting compared to their significance as indicators. The total number of the species was also considered as possible predictor in the regressions.

#### 2.4. Model choice and assessment

General linear models were chosen in a backward selection. We first calculated models with all the variables described as predictors, while avoiding combining *a priori* redundant ones. These were the following pairs: either the solar radiation potential or the south slope component, either the forest type or the proportion of broadleaved species, either the coverage of the vegetation layers or the LAI directly derived from them. Then we eliminated step by step those predictors that were not significant ( $p < 0.05$ ). In some cases, in order to make the obtained models easier to apply, we eliminated predictors from the model if they did not improve the coefficient of determination  $R^2$  by more than 1 or 2%, even if they were significant. In such cases, we display different versions of the model (Table 2). The distribution of the residuals and their linearity against predictors were assessed graphically. In some cases, as explained below, this was also used to choose between models.

The precision of the regression models was assessed internally according to their standard error and compared to the standard error of estimates obtained with hemispherical photography (with replicated photographs on each site). The error expected to affect predictions in an independent dataset was also calculated: for linear regressions, it is larger than the internal standard error by a factor  $\sqrt{(n+p+1)/(n-p-1)}$ , where  $n$  is the number of observations and  $p$  the number of independent variables.

#### 2.5. Model application

After obtaining a proper statistical model, we applied it to estimate the LAI for approximately 1000 sites across Switzerland for which all the necessary variables were available from vegetation surveys. The surveys had been made as described above for the 91 sites with hemispherical photographs (Table 1). They were carried out between 1972 and 2008 by 45 different authors. The area assessed on each site varied between 150 and 1000 m<sup>2</sup>. In many

cases the tree height was not directly measured, but was estimated by the observers. The majority of the sites were chosen to have a tree species composition close to natural, while 170 of them were taken from a regular 8 km × 8 km grid across the country. Most of these forests were of a mature type. Sites with only pioneer species or shrubs, as well as young forests with trees less than 15 m high, were excluded. Some mature forests also had trees smaller than 15 m, but this could be related to extreme site conditions (drought, water excess or high altitude) and these sites were included in the analysis. The final dataset contained 981 sites. The distribution of the different forest types according to altitude is shown on the X axis of Fig. 4, and those according to precipitation and to water balance in Figs. 5 and 6, respectively. Among the 981 sites, seven had a tree coverage estimated to 100%. Because a complete absence of gaps is not plausible and because it would result in an infinite LAI, these values were corrected down to the otherwise highest observed value of 98%, corresponding to  $L_a = 7.82$ . To test how sensitive the estimated LAI is to this assumption, the calculations were redone using a coverage of 99% ( $L_a = 9.21$ ).

In this large dataset, we searched for general patterns and for extreme LAI values in relation to site environmental variables not included in the regression model: the altitude, the  $F_{\text{Landolt}}$ ,  $N_{\text{Landolt}}$  and  $L_{\text{Landolt}}$  indicators (humidity, nutrients and light, respectively) and the water regime. To characterise the water regime, we calculated a site water balance from monthly differences between precipitation and potential evapotranspiration. In its iterative calculation, this balance was constrained within the water-holding capacity of the soil. The procedure was adapted from Grier and Running (1977), with the difference that the years were calculated from the first month in fall when precipitation exceeded evapotranspiration. The water-holding capacity was derived from the soil map of Switzerland (OFS, 2000), which takes into account the soil depth, the specific holding capacity and the stone content. Meteorological data were taken from the period 1961 to 1990, and spatially interpolated according to Thornton et al. (1997). The potential evapotranspiration was calculated according to Jensen and Haise (1963).

### 3. Results

#### 3.1. Leaf area indices and gap fractions obtained with hemispherical photography

The effective LAI of the 91 sites with photographs was in the range  $1.2 \leq L_e \leq 7.2$ , with an average of 4.1. The standard deviation of the LAI between single photographs within sites was 0.6. Total gap fractions in vertical projection were in the range  $0.9\% \leq T \leq 71\%$ , on average 17%. After clumping correction according to Chen and Cihlar (1995), the LAI values were  $1.5 \leq L_c \leq 7.3$ , on average 4.4. The large gaps separated by this method were  $0.03\% \leq G \leq 67\%$ , on average 9.8%.

Excluding the large stems from the analysis by painting them on 20 photographs resulted in lower LAI values. The effect of hiding the stems was linear:

$$L'_e = 0.99L_e - 0.05 \quad (6)$$

where  $L_e$  is the effective LAI of the original photographs and  $L'_e$  the value obtained after excluding the large stems. This relation was exactly the same for the 10 sites with the smallest trees as for those 10 with the tallest trees. The average LAI reduction following stem exclusion was  $0.09 \pm 0.07$ .

#### 3.2. Models predicting the gap fractions and LAI

For each dependent variable derived from the hemispherical photographs, the vegetation coverage above 1.5 m was always a

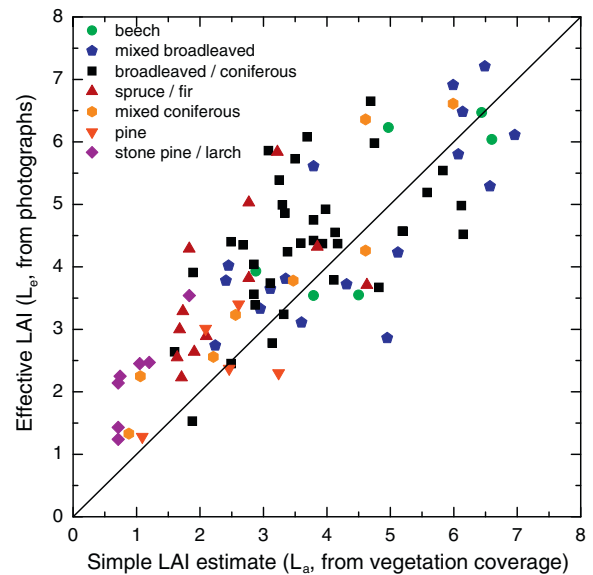
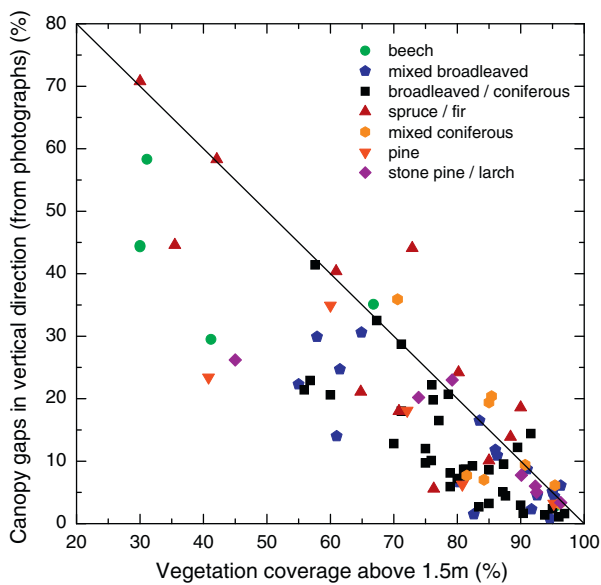


Fig. 2. Relationship between the LAI estimate directly obtained from the vegetation coverage above 1.5 m ( $L_a$ , see Eqs. (3) and (4)) and the effective LAI ( $L_e$ ) obtained from hemispherical photographs. See Table 2 for the regression model including these variables.

strong predictor (Table 2). The LAI values calculated from the photographs (both effective,  $L_e$ , and corrected for clumping,  $L_c$ ) were predicted better when the log transformation of Eq. (3) was used rather than the coverage itself. This was apparent in terms of  $R^2$  (gain of 0.02), and also because the coverage model produced a curved pattern in the residuals, while the residuals of the transformed model did not show any structure and had a distribution very close to normal. The vegetation cover below 1.5 m was also included in the statistical models, but with the opposite sign: the denser the low vegetation, the lower the LAI derived from the photographs. The height of the trees was also included in these models. The south slope component was included in the model of the effective LAI ( $L_e$ ). The potential solar radiation (Eq. (1)) could have been used instead of the south component, but it would have resulted in a slight non-linearity of the residuals. These topographical variables could also be removed without much affecting the coefficient of determination. A further reduction of the model to retain only  $L_a$  would, however, have decreased this coefficient to  $R^2 = 0.58$  (Fig. 2).

Simple regressions based on the vegetation cover and tree height showed a standard error of nearly 0.8. Thanks to the relatively large number of sites, their prediction error of 0.83 was not much larger. The within-site standard deviation between the hemispherical photographs was 0.6. Using the regression is thus slightly less precise than taking one photograph per site. This comparison, however, does not take into account the fact that hemispherical photographs can also be biased, for example if the sky condition is not optimal, which would reduce the accuracy of site averages.

The observed coverage of the high vegetation ( $C_a$ ) was also a strong predictor in the regression models of the vertical gap fractions, both for the total ( $T$ , Fig. 3) and for the large gaps ( $G$ ). As for the LAI models, the coverage of the low vegetation ( $C_b$ ) entered the model with the opposite sign. Landolt's ecological index for nutrients ( $N_{\text{Landolt}}$ ) was present in the regressions of the gap fractions, but it was possible to simplify the models to include only the coverage of the high vegetation without losing much precision. For the total gap fraction ( $T$ ), the forest type was significant and could be used alternatively in the model. The main effect concerned the pine forests, which have a larger gap fraction than the other forest types with the same observed tree coverage.



**Fig. 3.** Relationship between the vegetation coverage above 1.5 m ( $C_a$ , see Eqs. (3)–(5)) and the canopy gaps in a vertical direction derived from the hemispherical photographs. See Table 2 for the regression model including these variables.

Not significant for any of the models were the region, the altitude, the proportion of broadleaved species, and the number of species in the herb layer. In most cases, it was possible to obtain a regression model with an  $R^2 \geq 0.7$  using only a combination of the vegetation coverage above and below 1.5 m and of tree height. The only exception was the regression describing the large gaps in the vertical projection. In this case, it was also observed that the residuals were not normally distributed, but had a right tail with one standardised value of 2.6 and one of 4.0 (resulting from a very open canopy). No simple variable transformation was found that could correct this problem.

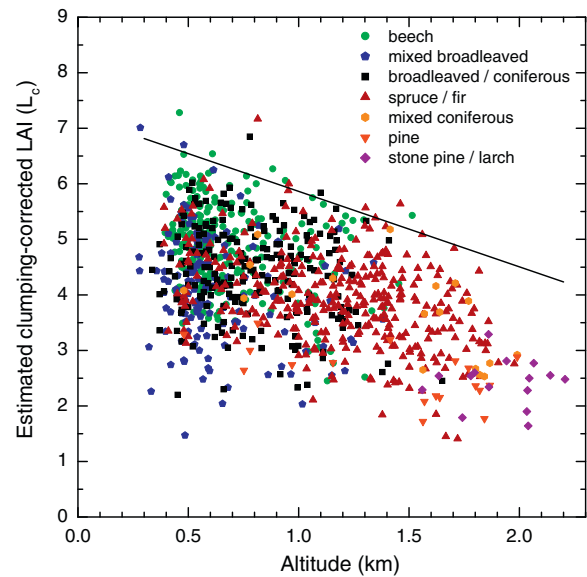
### 3.3. Model application to 981 sites

Applying the regression for  $L_c$  (Table 2) to the 981 forest sites gave clumping-corrected LAI values in the range  $1.4 \leq L_c \leq 6.7$ , with an average of 4.2 if we corrected to 98% the seven tree coverages recorded as 100%. Assuming instead 99% gave the same average but a maximum of 7.2, i.e. the range was very similar to that of the 91 photography sites. When analysing the extreme LAI values, both assumptions led to the same qualitative interpretations but to small differences, not exceeding 0.3 units. In the following, we chose to present the results obtained with 100% coverages corrected to 99%.

When plotted against the altitude (Fig. 4),  $L_c$  clearly decreased and its range narrowed. This trend arose because both the maximum tree coverage and the maximum tree height decreased with altitude (not shown separately here). A relation between precipitation and  $L_c$  was only apparent for sites with less than 1000 mm annual precipitation (Fig. 5). A limitation due to water availability was also evident when comparing  $L_c$  with another independent variable, the site water balance (Fig. 6). Our data are in good agreement with the relationship for maximum LAI developed in Oregon (USA), as first described by Grier and Running (1977), and then corrected by Waring and Running (2007):

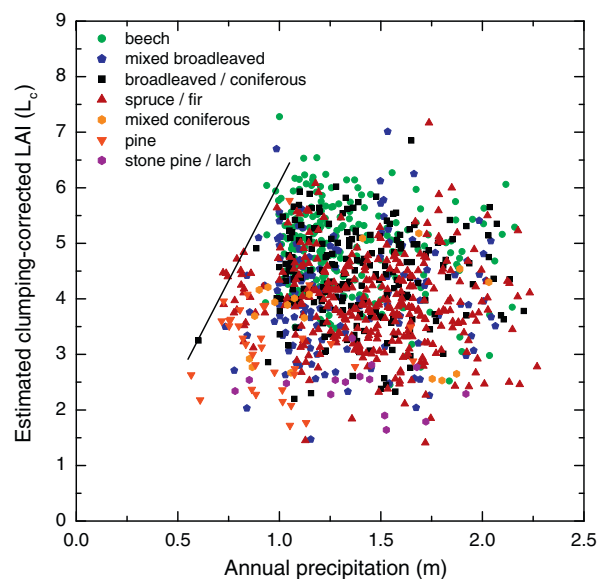
$$L_c \leq 6.8 + 5.6B \quad (7)$$

where  $B$  is the site water balance in m. At positive water balances, the range of  $L_c$  narrowed, but it is not possible to tell if this corresponds to a true limitation due to excessive water, to a correlation between the water balance and the altitude, or merely to a lim-

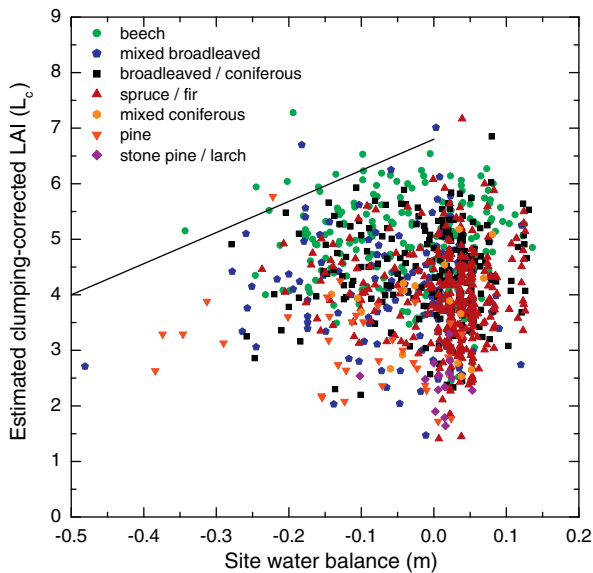


**Fig. 4.** LAI (corrected for canopy clumping) obtained through multiple regression (Table 2) as a function of the site altitude. A quadratic regression based on the maximum LAI per each of 20 equiponderant altitude classes ( $h$  in km) is shown as a line ( $L_c = 7.32 - 1.36h$ ,  $R^2 = 0.67$ ,  $p < 0.001$ ).

ited number of data. The humidity index  $F_{Landolt}$ , however, clearly showed that both dry and wet sites had a lower maximum LAI compared to mesic sites (Fig. 7). To check the causes of these limitations, we examined more closely all the sites with LAI values close to the maximum for their specific humidity index. The coverage of the tree layer decreased when moving from mesic to wet sites ( $F_{Landolt} > 3$ ), but the tree height was not particularly affected. The wettest sites all presented signs of hydromorphism in the soil profile, most of them being Gleysols. With drier sites ( $F_{Landolt} < 3$ ), in contrast, the observed coverage of the tree layer remained relatively high, but the trees were smaller. None of these soils showed signs of hydromorphism, indicating that they were mainly influenced by precipitation and not by stagnant water. The same applied to those sites close to Grier and Running's regression in Fig. 6.



**Fig. 5.** LAI (corrected for canopy clumping) obtained through multiple regression as a function of the annual precipitation. A linear regression based on the maximum LAI per each of 10 equiponderant precipitation classes ( $P < 1$  m) is shown as a line ( $L_c = -0.98 + 7.07P$ ,  $R^2 = 0.71$ ,  $p = 0.002$ ).



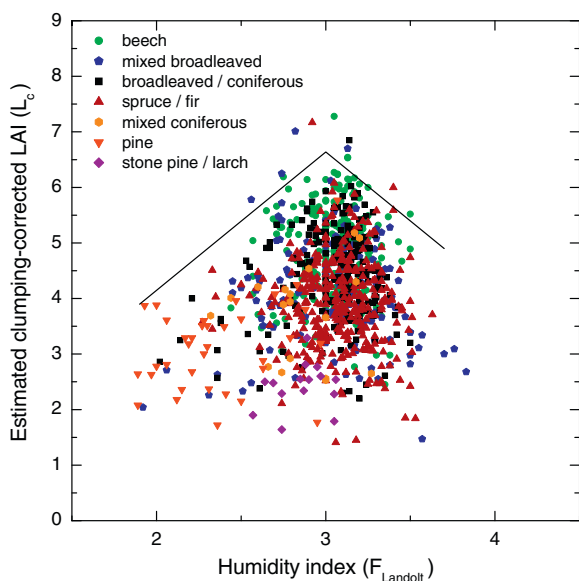
**Fig. 6.** LAI (corrected for canopy clumping) obtained through multiple regression (Table 2) as a function of the site water balance (see methods). The line corresponds to the equation of Waring and Running (2007):  $L_c = 6.8 + 5.6B$ , with  $B$  the water balance in m.

Landolt's light index  $L_{\text{Landolt}}$  was negatively correlated with the estimated LAI values, but with a considerable scatter (Fig. 8 of supplementary material,  $R^2 = 0.26$ ). The nutrient index  $N_{\text{Landolt}}$  showed a weaker relationship with the LAI, with even an apparent decrease at  $N_{\text{Landolt}} > 3.1$ , approximately (Fig. 9 of supplementary material). The pattern was quite similar to the one observed for the humidity index and  $N_{\text{Landolt}}$  was indeed clearly correlated with  $F_{\text{Landolt}}$  ( $R^2 = 0.45$ ).

## 4. Discussion

### 4.1. Regression models

The hemispherical photographs analysed in the present study covered a broad range of leaf area indices. Indirect methods in



**Fig. 7.** LAI (corrected for canopy clumping) obtained through multiple regression (Table 2) as a function of Landolt's humidity index  $F$ . A non-linear regression based on the maximum LAI per each of 20 equiponderant  $F$  classes is shown as a broken line ( $L_c = 6.64 - 2.49|F - 3.00|$ ,  $R^2 = 0.43$ ,  $p = 0.002$ ).

general (review by Bréda, 2003) and hemispherical photography in particular have often been shown to underestimate the LAI of dense canopies (Martens et al., 1993; Chen et al., 1997; Planchais and Pontailier, 1999). Among our 91 sites, we found maximal values between 7 and 8. These, however, could only be obtained by applying appropriate techniques, especially by choosing an exposure that excludes light blooming and by taking the effect of ground slopes into account (Schleppi et al., 2007; Thimonier et al., 2010). Scurlock et al. (2001) compiled some 200 values for each forest type of the temperate zone, either deciduous broadleaved or evergreen coniferous. After removing outliers (mainly from older publications), they found LAI values of  $5.1 \pm 1.6$  (average  $\pm$  standard deviation) and  $5.5 \pm 3.4$ , respectively. The highest value reported by Waring and Running (2007) for conifers in Oregon, USA was 8. The same maximum was found for mixed forests in France by Le Dantec et al. (2000). Compared to these and similar studies, the range observed in our study thus appears perfectly plausible.

The regressions developed from the hemispherical photographs enabled us to estimate the canopy openness and leaf area index over a very wide range of forest types across Switzerland for which vegetation surveys were available. A somewhat similar approach was used by Dahlberg et al. (2004) to estimate through regression not only the leaf area, but also the biomass of trees and shrubs. For shrubs, they also found that the vegetation coverage and LAI are related. This is self-explanatory since this compares two different methods assessing essentially the same parameter, the leaf area. For trees, Dahlberg et al. (2004) also found the height to be a factor affecting the leaf area, but they worked with the area per tree. Because differences in stocking density can also affect the LAI (e.g. Le Dantec et al., 2000), this height effect at the tree level does not imply that it is also the case at the stand level. The importance of the tree height in our regression models for the LAI is somewhat surprising, especially because this factor does not enter the regressions for the gap fractions (Table 2) and is not related to the leaf angle (data not shown). In our regressions, it may essentially be a confounding factor for drought or for all environmental factors changing with altitude. These factors are known to limit tree height, but the altitude itself was not nearly as good a predictor. Tree height may be a strong predictor because it combines the effect of altitude with those of exposition and soil fertility, as it is the case for the forestry site indices based on height growth speed. Alternatively, tree height may be effective as a correction for some optically induced bias in the observation of the vegetation coverage. Observers may indeed tend to underestimate the coverage of the trees if the crowns are higher above them. Why tree height is so important is difficult to explain, but in any case it cannot be ignored without impeding the precision of the models.

The coverage of the low vegetation appears in the regression models for LAI with a negative sign. This is obviously due the higher layer shading the lower layer, as already observed e.g. by Saetre et al. (1997), Bartemucci et al. (2006) or Tinya et al. (2009). More coverage of the low vegetation therefore to some extent indicates less coverage of the upper vegetation layers.

The geophysical site characteristics, region, forest type and ecological indices based on the botanical composition of the ground vegetation were either not significant or could be removed from the models without substantial loss of precision. This does not mean that these variables are not at all related to canopy openness and to the LAI, but the stand characteristics turned out to be better predictors. For example, coniferous forests often have lower LAI values than broadleaved forests and, taken alone, the proportion of broadleaved species would be a highly significant factor explaining the LAI. Beside vegetation cover and tree height, however, this variable has no additional informative value and thus it does not show up in the models. The same applies to the classification of forest

types and regions, and to Landolt's indices, which are all correlated to the effective LAI, but none is as good a predictor as the chosen stand characteristics.

In a first approximation, it could be expected that the vertical canopy openness derived from the photographs should be directly related to the vegetation cover above 1.5 m:  $T = 1 - C_a$ . In our regression, when the observed vegetation cover tends towards 100%, the canopy openness of the photographs indeed tends towards zero. However, a vegetation cover assessed to 50% corresponds in our model to an openness of only 35%. The only explanation of this systematic discrepancy is that observers tend to overestimate the proportion of gaps in the canopy (compared to the analysis of photographs). In our dataset, the lowest  $C_a$  values are 30% and there is no evident sign of non-linearity in the observed range. Because any observer would obviously estimate correctly a coverage of zero in the absence of trees and shrubs, this means that there must be a non-linearity between the observed and the measured values in very open canopies. Therefore, it is clearly not advisable to extrapolate the given regression for  $C_a < 30\%$ .

Similarly, the LAI should essentially be the same if derived either from the vegetation cover above 1.5 m ( $L_a$ ) or from the photographs ( $L_e$ ). We do indeed find a relationship between  $L_a$  and  $L_e$  (Fig. 2), but with some scatter. The leaf angle plays a role in this comparison since an erectophile foliage leaves more sky visible in a vertical direction than a planophile foliage with the same LAI. In the direct calculation of  $L_a$  out of the coverage  $C_a$ , however, the mean leaf angle is always supposed to be  $\alpha = 54^\circ$ , with a projection coefficient  $G = 0.5$  (Campbell, 1986). The leaf angles of the sites retained for our study were, on average,  $\alpha = 52^\circ$ , but varied within the limits set as  $25^\circ \leq \alpha \leq 75^\circ$ , corresponding to  $0.85 \geq G \geq 0.24$ . This variation, along with other random sources of errors, can thus explain the scatter observed in the relationship between  $L_a$  and  $L_e$  quite well. There is, however, also a systematic difference, with  $L_e$  being on average 0.6 units higher than  $L_a$  (4.05 vs. 3.45). We checked whether this could be caused by the stems, which are visible on the photographs but which were not counted as coverage by the observers. Excluding the large stems on the photographs from the analysis did lower the calculated LAI, but the difference was only approximately 0.1, which is not enough to explain why  $L_e$  exceeds  $L_a$  by 0.6. The main reason for this discrepancy is thus the overestimation of the gap fraction by the observers, as already noted above.

To make the vegetation surveys comparable with the hemispherical photographs, we had to divide the shrub layer into a lower and a higher sub-layer and to add those to the herb and tree layer, respectively. This approach may appear complicated and not highly reliable. It must be noted, however, that this was only necessary for the development of the regression models. For the application of the regressions, it is perfectly possible to consider only the coverage of the trees to derive their own LAI. Alternatively, the LAI of trees and shrubs together could be derived from their combined coverage (which is, obviously, not equal to the sum of each coverage because of their mutual shading, see Eq. (4)). From this point of view, the LAI derived from our regression has even an advantage over the photographs because it enables us to choose if the shrubs should be included or not.

#### 4.2. Applying the model

Applying the obtained regression models to nearly 1000 forest sites across Switzerland generated LAI values that ranged from very low to high. All were plausible. Comparing them to environmental parameters not included in the regressions enabled us to discern several patterns, representing an indirect validation of the model. None of these patterns (Figs. 4–7) indicated a narrow relationship, which was certainly due to the effects of forest management and, in some cases, of disturbances. These factors could not be quanti-

fied for this study, but since they always tend to reduce the LAI, their effect can be removed by considering only the maximal LAI values. Due to the large number of sites considered, the analyses based on maxima per classes of independent variables were not only meaningful but also statistically significant (Figs. 4, 5 and 7).

The broad range of the sites studied revealed first the effect of the altitude as a limiting factor for the LAI. Low values of 2 or even less can be observed at any altitude, but maximum values are clearly smaller at higher altitudes (Fig. 4). From 400 to 2000 m a.s.l., the maximal LAI is decreasing by approximately one third. At different latitudes and in other climatic zones, this relationship can be shifted, as for example in Tibet, where the decrease in LAI appears to start near 3000 m a.s.l. (Luo et al., 2004). Nevertheless, altitude can clearly limit the amount of foliage in forests and this limitation can be quantified. This effect is directly related to the fact that mountain forests tend to have more open canopies and shorter trees, but it may also be due to a reduction in the size of single leaves at lower temperatures, as observed by Meier and Leuschner (2008).

Across different forest types, Granier et al. (2000) found that LAI (up to approximately 6) and transpiration correlate well as long as enough water is available. High LAI values mean thus not only an increased interception of precipitation but also a faster depletion of soil water. According to our dataset, a water shortage limits LAI when annual precipitation is lower than 1000 mm (Fig. 5). A similar conclusion was drawn by Köstner (2001), based on observations in southwestern Germany. The effect of the precipitation amount may be different in other climatic zones, but the site water balance according to Grier and Running (1977) seems to be a robust parameter to quantify LAI limitation by drought. Many values of our dataset can be observed below the regression line of Waring and Running (2007), but very few above (Fig. 6). Le Dantec et al. (2000) showed that drought stress limits the LAI in the following year. Dobbertin et al. (2010) showed that irrigation can increase the LAI of *Pinus sylvestris* in a dry alpine valley (Valais, Switzerland). More generally, McDowell et al. (2008) described lower LAI values under recurrent drought stress as a mid- and long-term strategy of trees to reduce their water needs. Our results are in line with these findings.

Our dataset shows that LAI can also be limited by an excess of water. The range of positive values of the site water balance is not broad enough to draw quantitative conclusions, but Landolt's humidity index of the ground vegetation shows a clear, almost symmetrical pattern. Botanical compositions typical of either dry or wet conditions both correspond to lower LAI maxima. Towards the wet end of the scale, the observed decreasing tree density corresponds to a progressive change from closed forests towards more or less open sites, often with a small-scale topography enabling tree growth on mounds but not in wet soil depressions. Some other studies failed to find an effect of water availability on LAI (e.g. Hebert and Jack, 1998; Leuschner et al., 2006). An important difference, however, is that they studied single species, while our study covers a broad range of forest types and species.

Nutrients have also been shown in several studies to correlate with the LAI of forests (Fassnacht and Gower, 1997; Hebert and Jack, 1998; Luo et al., 2004). In our study, the LAI showed a weak optimum curve in relation to the nutrition index of the vegetation. We see two main reasons for this pattern. Firstly, Landolt's index is not a precise indicator because it does not distinguish between different nutrients. Secondly, it is clearly correlated with the humidity index, showing that it is very difficult to use a vegetation survey to assess the nutrient status of a site separately from its water status. The light index of the ground vegetation is negatively correlated to the LAI. This can be considered as a shading effect, since a denser tree canopy limits the availability of light for the ground vegetation.

One of our most striking findings was that the observed relationships were practically independent of the forest types. Differences

between forest types obviously exist, but they mostly build a continuum within the effects of site variables on LAI and do not appear as a distinct factor, as can be seen studying Figs. 2–7. For conifers, this confirms the conclusion of Grier and Running (1977) that the relationship between site water balance and leaf area is largely independent of the species. The regressions obtained here, as well as their application show that this is also true for broadleaved trees. Our conclusions are thus in line with those drawn by Granier et al. (2000), who found that the water conductance of a forest canopy (standardised to defined meteorological conditions) is related to the LAI, and that the reduction of this conductance by soil drying is independent of the species, regardless of whether it is broadleaved or coniferous.

The patterns we observed appear to be quite robust. Some constraints arising from our methodological choices should, however, not be forgotten. First, we excluded young stands from our study, as well as sites with only shrubs and no trees. Our observations are thus not directly applicable to such sites. They should also not be extrapolated to sites with less than 30% tree coverage. Specific factors of the ground vegetation may also affect the predictions of our models. If surveys are conducted in the spring, then geophytic species are likely to induce slightly underestimated LAI values because they are likely to cover large areas before the development of deciduous tree foliage. In contrast, forests growing on boulder landscapes have less coverage of herbs than could be expected from the light conditions, which may result in LAI overestimations. The maximal errors due to the coverage of the low vegetation is however limited because the corresponding factors in the regressions are an order of magnitude smaller than those of the vegetation above. In dense canopies, a critical point in the application of our regressions of LAI is the correct estimation of coverages close to 100%, i.e. gap fractions close to 0. Because of the logarithm transformation, small errors in the observed gap fraction result in large errors for the LAI. This problem, however, also exists for any other method based on the measurement of gap fractions.

## 5. Conclusion

We have developed a method to estimate the gap fraction and LAI of mature forests based on simple stand parameters that can be directly estimated in the field. Compared to values obtained with hemispherical photography, LAI was predicted with a high coefficient of determination ( $R^2 > 0.7$ ) using the following variables: coverages of the tree, shrub and herb layers, and tree height. The method appears to be relatively precise and robust across different types of semi-natural forests, including broadleaved, coniferous and mixed stands. When applied to almost 1000 sites across Switzerland, the regression model produced results that were all in the expected range. The LAI estimates obtained showed perfectly plausible relationships with the altitude and with variables describing the site water availability.

Compared to optical measurements (including hemispherical photography), our method is fast and inexpensive. It has the advantage that the observations are almost independent of the weather, whereas optical measurements can be strongly biased by irregular sky conditions. Another advantage is that observers can choose which vegetation layer they estimate, allowing an assessment of the LAI of the trees only or a combined value for trees and shrubs. This is also an advantage compared to remote sensing, which is, in the best case (multi-angle sensing), able to separate only the tree and herb layers (Pisek et al., 2010). Another difference is that multi-angle remote sensing has so far, due to its limited resolution, described only large forested landscapes in the order of magnitude of km<sup>2</sup>, while vegetation surveys are site-specific. This means that such surveys can be carried out at a spatial resolution adapted to the

heterogeneity of the forests, which depends on both their natural site conditions and their management. Such an approach appears very promising for obtaining reliable estimates of the LAI for many sites at little cost, and then using these data to run ecosystem process models at the stand level. A further development could be to combine these data with forest site maps to allow applications on large regional or national scales.

Our study was conducted only in Switzerland and its results are thus not directly applicable outside Central Europe. It would certainly be interesting to test how far they are valid across Europe or even on other continents. This could be done by applying the methods described here to existing research networks like BELMANIP (Baret et al., 2006). With the large number of sites already assessed and referenced in national databases of vegetation surveys, comparisons with remote sensing would also be of great interest, at least in regions where the spatial resolution of the latter is not a problem.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.11.013.

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