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A comparison of three indirect methods for estimating understory light at different spatial scales in temperate mixed forests

Flóra Tinya[1,2], Barbara Mihók[1], Sára Márialigeti[1], Zsuzsa Mag[1], Péter Ódor[1,3]

[1]Department of Plant Taxonomy and Ecology, Loránd Eötvös University, Pázmány P. sétány 1/C, H-1117 Budapest, Hungary

[2]Department of Plant Pathology, Corvinus University of Budapest, Ménesi út 44., H-1118 Budapest, Hungary

[3]Corresponding author; Tel.: +36 12090555/1711, Fax: +36 13812188, E-mail: ope@ludens.elte.hu

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Abstract: Three indirect light measurement methods were compared in mixed deciduous and coniferous forests with heterogeneous stand structure: tRAYci - a spatially explicit light model calculating percentage of above canopy light (PACL); LAI-2000 Plant Canopy Analyzer measuring diffuse non-interceptance (DIFN); and spherical densiometer estimating canopy openness (CO). Correlations between the different light variables were analyzed at several spatial scales (at 5 x 5, 10 x 10, 15 x 15, 20 x 20 and 30 x 30 m^2). Relationships between light variables and the cover of a light flexible plant, blackberry (*Rubus fruticosus* agg.), as a potentially sensitive response variable for light conditions were also investigated. LAI-2000 (DIFN) and tRAYci (PACL) seemed the most appropriate for the description of the light environment in the investigated stands. DIFN and PACL had stronger correlations with each other and with blackberry cover than CO. Spatial heterogeneity of light (expressed with coefficient of variation) showed much stronger correlations than mean values both between the methods and between light intensity and *Rubus* cover. The correlation values between the methods increased towards coarser scales (from 5 x 5 to 30 x 30 m^2), while the correlation between light intensity and blackberry cover had a maximal response at the scale of 20 x 20 m^2 if a lower resolution of light estimation was used, and had also a maximum at smaller scales if the light was calculated for more points per plot by tRAYci. LAI-2000 can be recommended for the comparison of different stands, however, for fine scale description of light conditions of a stand tRAYci seems to be more appropriate.

Nomenclature: Nomenclature for vascular plants follows Tutin et al. (1964-1993).

Abbreviations: DIFN–Diffuse Non-interceptance, PACL–Percentage of the Above Canopy Light, CO–Canopy Openness, LAD–Leaf Area Density, DBH–Diameter at Breast Height

Introduction

In temperate deciduous forests light is one of the most important factors in the establishment and growth of seedlings and regeneration (Canham and Marks 1985, Ke and Werger 1999). It also determines the cover and composition of herbaceous species, which differ substantially in their functional responses to light conditions (e.g. sun-tolerant, light-flexible, shade-tolerant herbs, Collins et al. 1985). The amount and the distribution of understory light is determined both by the geographical location and the structural characteristics of the forest (density, compositional and structural diversity of trees, number of crown layers, presence of understory saplings, etc., Anderson 1966, Martens et al. 2000, Comeau and Heineman 2003, Valladares and Guzman 2006). The extent and spatial scale of light heterogeneity mainly depends on the natural disturbance regime (e.g. fine-scale gap dynamics or large-scale windstorms) and the management of the forest (West et al. 1981). In managed forests, in order to maintain floristic diversity and ensure the suitable regeneration of understory trees it is necessary to provide information for the silvicultural management on preferable light conditions and stand structure (Comeau 2000).

In recent decades, several light-measurement and estimating methods have been developed (Welles 1990, Comeau 2000). Many spatial and temporal replications of instantaneous direct measurements could supply the most accurate results (Messier and Puttonen 1995, Parent and Messier 1996, Messier and Parent 1997). However, the sample size is limited using these time consuming methods. Therefore short-term datasets may not reflect the long-term pattern of incident light because of the spatial and temporal variations of light environment (Stadt et al. 1997, Gendron et al. 1998, Brown et al. 2000, Englund et al. 2000, Hale and Edwards 2002). Using indirect methods, one light assessment in time can estimate the relative light conditions for the whole vegetation period. These methods, as LAI-2000 Plant Canopy Analyzer, canopy models (Cescatti 1997a, Brunner 1998, Comeau et al. 1998a, Stadt and Lieffers 2000, Silbernagel and Moeur 2001, Coates et al. 2003) and hemispherical photography estimate the relative light conditions measuring the shading effect of canopy and topography. Canopy openness can be estimated by spherical densiometer.

LAI-2000 Plant Canopy Analyzer measures instantaneous radiation (wavelength < 490 nm) (LI-COR Inc. 1990). Its sensor contains hemispherical optics and five detectors which measure simultaneously incident light in different zenith angles (from 0^o to 74^o zenith angle), in five concentric annuli. With two devices, simultaneous above- and below-canopy measures can be carried out. The instrument calculates the diffuse non-interceptance (DIFN) comparing above- and under-canopy light intensity, which is conceptually similar to the instantaneously measured diffuse incident light on overcast days (Gendron et al. 1998). With included software it is possible to compute leaf area index from DIFN values (Welles and Norman 1991).

Spherical densiometer is a very simple and inexpensive manual device in forestry practice to estimate the cover percentage of canopy openness (CO) in forest stands (Lemmon 1956, 1957). It consists of a convex mirror with a grid of 24 squares engraved on the surface. The observer estimates canopy cover at four equally spaced points in each square holding the device horizontally, in four directions. However, its field-of view extends only from 0^o to 50^o zenith angle, canopy openness estimations reasonably give positive correlation with incident light (R^2>0.8, Englund et al. 2000).

In recent decades, spatially explicit forest stand models using a crown representation of individual trees have made it possible to model light environment in a forest stand (Cescatti 1997a,b, Brunner 1998, Comeau et al. 1998a, Martens et al. 2000, Mizunaga 2000, Stadt and Lieffers 2000, Silbernagel and Moeur 2001, Coates et al. 2003). They can be used for describing the pattern of canopy gaps influencing the understory vegetation (Silbernagel and Moeur 2001), modeling regeneration and forecasting the population dynamics of trees (Stadt and Lieffers 2000, Coates et al, 2003), investigating the effect of forest management (e.g. thinning) to light conditions (Mizunaga 2000), and also for modeling the light capture of individual trees (MacFarlane et al. 2003). Their reliability is relatively good, compared to growing season irradiation (Gendron et al. 1998), to hemispherical photographs (Gersonde et al. 2004) and to LAI-2000 (Pinno et al. 2001), but sometimes they can under- or overestimate light which indicates that they need further refinement (Comeau et al. 1998b). The model tRAYci calculates the percentage of the above canopy light (PACL) for any point of the modeled stand separating the total irradiation to direct and diffuse components (Brunner 1998).

Another widely used method for estimating relative irradiance is hemispherical photography (Anderson 1964, Gendron et al. 1998, Brown et al. 2000, Frazer et al. 2001, Hale and Edwards 2002). However, according to some studies, it does not offer a reliable estimate in heavily shaded sites, it is usually used in more open stands or in gaps (Chazdon and Field 1987, Roxburgh and Kelly 1995, Hale 2003). We found also in our preliminary studies that it did not correlate with any other techniques in relatively closed forests.

There is an increasing number of comparative studies of light-measurement and -estimation methods in various light environments (Gendron et al. 1998, Machado and Reich 1999, Englund et al. 2000, Engelbrecht and Herz 2001, Ferment et al. 2001, Frazer et al. 2001, Bellow and Nair 2003, Hale 2003, Rhoads et al. 2004, Mihók et al. 2007), but since the detected relationships are only valid for the studied forest type, the instruments must be tested in various types of stands. Further investigations are also necessary for the light models, because compared to the number of different models, the number of their applications in different forest types is very low (Comeau et al. 1998b, Gendron et al. 1998, MacFarlane et al. 2003, Gersonde et al. 2004, Pinno et al. 2001).

A widely used procedure to compare different indirect techniques is to compare the light values estimated by different methods to light measured by a direct light meter (Gendron et al. 1998, Machado and Reich 1999, Engelbrecht and Herz 2001). For lack of such a possibility the light estimated by the investigated indirect methods can be compared to each other (Englund et al. 2000, Ferment et al. 2001). Because many species are known as light flexible plant, a third solution could be to use the cover of such a species, as a potentially sensitive response variable for light conditions.

Beside the amount of light also its spatial heterogeneity can be an important component of understory light environment, because many species, which live in smaller or larger gaps, may be related to forests with heterogeneous light conditions (Valladares and Guzman 2006). Gaps can be created by one or more trees, but smaller light areas can be established by the irregular crown shape of individual trees, the occurrence of tree species having a sparser crown, or the lack of second overstory or shrub layer. These small light patches are particularly important in closed stands, where the amount of light is usually relatively low. Most of the forest herbs are clonal (Klimes et al. 1997), so they can easily extend their cover, if they find a more open patch in the understory. The applicability of these methods for light heterogeneity estimation is rarely studied. It is also little explored, whether light flexible plants are related to the mean or the spatial heterogeneity of light.

Although, there are some studies that investigated the use of the methods at different temporal scales (Machado and Reich 1999, Engelbrecht and Herz 2001), few papers dealt with light measurements at different spatial scales (Engelbrecht and Herz 2001, Jelaska et al. 2006). However it can be important because species of different microhabitats (shady areas, gaps, larger open fields) can be related to light at different spatial scales (Tinya et al. in press). The scale of their response to light can be dependent also on the size of the polycormons created by a species.

The questions of the present study are the following:

i) Which is the most useful indirect technique among LAI-2000, tRAYci model, and spherical densiometer to compare the understory light conditions of different forest stands? In case of tRAYci, are there any differences in the usefulness of the model if the height of the sampled points or the spatial resolution of sampling are changed?

ii) Is the mean or the heterogeneity a more sensitive descriptor of light conditions in the course of comparisons of the different methods?

iii) How do the used different spatial steps influence the studied relationships?

To answer these questions correlations were calculated i) between light variables (mean and coefficient of variation) estimated by the three methods, and ii) between light variables estimated by the different methods and the cover of a light flexible plant, blackberry (*Rubus fruticosus* agg.). All these calculations were carried out at five different spatial steps.

Methods

Study area

The study area was located in the Őrség National Park, a western area of Hungary (N 46°51'-55' and W 16°07'-23'). The elevation is between 250-350 m above sea level and the topography consists of hills and wide valleys. Mean annual precipitation is ca. 800 mm, mean yearly temperature is 8.9-9.2 °C, and the western part of the region has a cooler and more humid climate than eastern parts (Marosi and Somogyi 1990). The bedrock is alluviated gravel mixed with loess. The soil is acidic and nutrient poor, the most common soil type on hills is pseudogleyic brown forest soil, while in the valleys mire and meadow soils can be found.

The characteristic vegetation types of the region are deciduous-coniferous mixed forests, dominated by beech (*Fagus sylvatica*), sessile and pedunculate oak (*Quercus petraea et Q. robur*), hornbeam (*Carpinus betulus*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and the proportion of different mixing species (*Betula pendula*, *Populus tremula*, *Castanea sativa*, *Prunus avium*, etc.) is also high (Tímár et al. 2002). Forest management is heterogeneous, both spontaneous stem selection system resulting in uneven aged stands and shelterwood management system with a rotation period of 70-110 years do occur (Matthews 1991). The herbaceous vegetation is formed by mesophilic and acidophilic species, the shrub layer mainly consists of beech, hornbeam and the saplings of mixing species. The cover of herbs and tree regeneration are very variable among stands.

Data collection

23 stands representing different tree species combinations and stand structure were selected (Table 1.). Further criteria of the site selection were as follows: dominant trees older than 70 years, more or less flat slope and absence of water influence. In each stand, a block of 40 x 40 m^2 (0.16 ha) was selected for stand structural measurements. In the center of the blocks, a quadrate of 30 x 30 m^2 was defined, where the light characteristics and the cover of herbs were measured in 36 adjoining 5 x 5 m^2 plots. Light conditions were characterized using three indirect methods: diffuse PACL was calculated by tRAYci, a spatially explicit light model (Brunner 2004), DIFN was measured by LAI-2000 Plant Canopy Analyzer (LI-COR Inc. 1990) and CO was estimated by spherical densiometer (Lemmon 1956).

For the tRAYci model, spatially explicit position of the trees which were larger than 5 cm in diameter at breast height (DBH) were mapped in the blocks in 2005 and 2006. Tree species, DBH, height, height of crown base, and crown radii to 4 directions were also recorded for each tree. To avoid large biases in the crown model, by measuring height of trees and height of crown base the upper and lower border of the coherent part of the crown was considered, and overhanging or separated branches were neglected. The directions of the crown radii measurements were determined as follows: The first was the direction of the longest radius, and then other three directions were always perpendicular to the previous. Crown radius was defined as distance of the margin of crown from the trunk. The border of the canopy was estimated visually (without using crown mirror). According to our preliminary study, visual estimation gave statistically similar results to estimation using crown mirror. For each individual tree, crown shape type was visually defined, based on the manual of the model (Brunner 2004). During the analysis, one shape type was used for a tree species in a stand. The thickness of the vertical shell layer was set 20% for the upper crown part and 0% for the lower part for all species. The leaf area density (LAD) of each species was determined based on published data and field experience (Table 2., Brunner et al. 2004, Gersonde et al. 2004, Lalic and Mihailovic 2004). Homogeneous patches of shrubs and saplings (woody plants smaller than 5 cm DBH, but higher than 0.5 m) were mapped. The position of saplings in the model was randomly distributed within the patches. In each patch, species, abundance and a common value of size parameters (tree height, canopy height and width, etc.) of saplings was recorded, so these size parameters were the same for each sapling within one patch. As the crown of the saplings are sparser than that of larger trees (based on field experiences), the LAD parameters were lower in the case of saplings than in the case of canopy trees of a species (Table 2). The direction and the slope of the maximum tilt were measured at every block. To avoid edge effects in light calculations, the real, mapped block was multiplied in the model to all spatial directions around the real block, to simulate the surrounding parts of the stand. Diffuse PACL was calculated in three different designs: i) in the center of the plots at a height of 1.3 m (comparable to the other two methods); ii) in the center of the plots at a height of 0.5 m (directly over the herb layer); iii) in a finer resolution: at a height of 0.5 m for 5 points per plot: the center and four points midway between the center and the corners of the plot (i.e. the mean of 5 calculations were used during the analyses). Diffuse PACL values were calculated for the period from 1st April to 31st October.

LAI-2000 measurements were conducted between June and August 2006. Three instantaneous measurements were taken in the center of each plot at 1.3 m height. The measurements were carried out under different sky conditions (from the standard overcast to the sunny weather), but always at dusk to avoid direct light getting into the sensor. A 270° view restrictor was also applied to mask the portion of the sky that contains the sun and the operator (LI-COR Inc. 1990). Reference above-canopy measurement was taken on open fields nearby. As these open areas were often not large enough, the view angle of the instrument was reduced to 58° from zenith by the exclusion of the sensor's outer ring from recording. So its view angle was similar to the densiometer's, which makes the measurements more comparable. ”Above canopy” measurements were taken in every 15 sec. during the below canopy measures, and ”above canopy” data were paired with the below canopy readings. The 1000-90 Communication Software was used to load the data to a PC, and 2000-90

Support Software was applied to match the above and below canopy data, eliminate the external ring and calculate DIFN values (LI-COR Inc. 1991, 1992).

CO was estimated by spherical densiometer in the center of the plots at 1.3 m height (similarly as LAI-2000) in the vegetation period of 2006. In each point, four measurements were carried out to cardinal directions. The instrument was used by six operators, but during a pilot survey they calibrated their estimates to each other.

As a biological reference to different light estimating methods, a typical light flexible plant of the understory was chosen: blackberry (*Rubus fruticosus agg.*, Fotelli et al. 2005, Mountford et al. 2006). This species is present in nearly all of the investigated stands (Table 1) and it is a dominant plant of the herbaceous assemblage. The cover of *Rubus* was visually estimated in each plot during the period from June to August 2006. It was evaluated originally in dm^2 in the field and transformed to percentage of the ground area for the analysis.

Data analysis

The relations between light variables of different methods (PACL, DIFN, CO) were analyzed by correlation analysis at more spatial scales. The relations between blackberry cover and light estimated by different methods were investigated similarly by correlation analysis. The used spatial steps were 5 x 5, 10 x 10, 15 x 15, 20 x 20 and 30 x 30 m^2. In each spatial steps stands were represented by one sampling unit and the number of samples was the same (23), only the size of the sampling units was changed merging the adjacent plots. Hereby, the spatial autocorrelations between sampling units of the same blocks and the effect of sample size for the correlations were avoided. Except the finest spatial step, not only the amount of available light (mean values of merged records), but also the heterogeneity of light within sampling units was used during the analyses. Heterogeneity was expressed as the merged record's coefficient of variation (Zar 1999).

The mean values and the variation coefficients of the studied light variables were compared by ANOVA.

As the investigated variables were significantly biased from normal distribution (based on Kolmogorov-Smirnov test with Lillefors correction) on several occasions during the correlation analyses, non-parametric Spearman rank-correlation was calculated in all cases (Zar 1999). The original cover data of blackberry were logarithmically transformed. The analyses were carried out by SPSS 14.0 for Windows program package (SPSS Inc. 2005).

Results

Descriptive statistics

At 30 x 30 m^2 spatial scale the mean of DIFN and CO values were 2.75% and 10.91%, respectively (Table 1). The mean of PACL values calculated by the tRAYci model were 14.18%, 14.19% and 14.21% for the height of 1.3 m, 0.5 m, and 0.5 m in five points per plot, respectively. The difference in the vertical positions and number of records did not influence the PACL values (ANOVA, $F_{(2,22)} = 0.00$, $p>0.1$). Estimating the relative amount of light, DIFN values were significantly lower than PACL and CO (ANOVA, $F_{(2,22)} = 62.7$, $p<0.001$). The coefficient of variation of DIFN (0.53) was significantly higher than that of PACL (0.28) and CO (0.29, ANOVA, $F_{(2,22)}$ = 14,32, $p<0.001$). The mean blackberry cover was 0.49 ± 1.27% (mean ± standard deviation).

Correlations between methods

Rate and significance of correlations between means of DIFN, PACL and CO variables varied depending on the methods and the spatial scale (Table 3). Strong positive correlations were found between DIFN and CO at the 30 x 30 m^2 scale, between PACL and DIFN at the 15 x 15, 20 x 20 and 30 x 30 m^2 scale, and between PACL and CO at every scale except 5 x 5 m^2. Highest positive correlation was found between DIFN and PACL at the 30 x 30 m^2 scale.

Light heterogeneity (expressed by the coefficient of variation within sampling units) showed much stronger positive correlations between the methods than mean values (Table 3). Strong positive correlations were obtained in all cases. The correlation coefficients were the highest at 20 x 20 m^2 scales in the case of DIFN – CO and PACL – DIFN, while at 30 x 30 m^2 scale in the case of PACL – CO. The strongest positive correlation was found between DIFN and PACL at the scale of 20 x 20 m^2 (r=0.831).

Relationship between variables of light and blackberry cover

There was no significant correlation between blackberry cover and the mean of any of the light variables (PACL, DIFN and CO), while using variation coefficient of the light values, significant correlations could be observed at all methods (Table 4). The strongest correlations of blackberry cover were observed with the PACL values calculating 5 data per plot. There was no considerable difference between the correlation coefficients calculating PACL values at 1.3 m or 0.5 m, but 5 points per plot gave higher correlation coefficients than only one point. Correlation values of CO were lower than those of PACL and DIFN.

Investigating the effect of spatial scales, cover of blackberry increased until 15 x 15 m^2, where it reached its maximum, and at coarser scales, it did not change considerably (Fig. 1). The variation coefficients of light variables showed a monotonous increase from finer to coarser scales at all methods. Considering only one sampling point per plot (DIFN, CO, PACL at 1.3 and 0.5 m height) in case of correlations between *Rubus* and the variation coefficient of light, the coefficients linearly increased with spatial steps until 20 x 20 m^2, and showed a maximum value around this scale. If we calculated light variables with tRAYci for five points per plot, the coefficient of correlation had a large improvement at finer scales (5 x 5 and 10 x 10 m^2).

Discussion

Comparison of techniques

According to other studies based on direct light measurements, the relative light intensity under closed canopy was below 6% both in deciduous (dominated by *Fagus*, *Populus* and *Acer* species) and coniferous (dominated by *Picea* species) forests (Constabel and Lieffers 1996, Emborg 1998, Messier et al. 1998). In Hungarian beech forests PACL values calculated from hemispherical photographs were below 10% under closed canopy, and could reach 10-36% in gaps, depending on the size of the gap (Mihók and Standovár 2005, Gálhidy et al. 2006, Mihók et al. 2007).

In this study, the mean values of PACL were found considerably higher (above 14%) than the DIFN (2.75%). The light values calculated by the model depend considerably on model parameterization. In the case of the tRAYci model, the PACL values depend considerably on LAD parameters. There are very few reported data for the value of the parameters (Brunner 1998, MacFarlene et al. 2003, Brunner et al. 2004, Gersonde et al. 2004, Lalic and Mihailovic 2004), and a published LAD parameter of a given species is not necessarily valid at all conditions. It would be possible to calibrate the LAD parameter of the species after measured leaf area index values (Brunner 1998, 2004), but it is labor-intensive, and requires mono-specific stands of all species, which is not achievable e.g. in cases of mixing species. Thus, the parameterization of tRAYci is complicated and this may cause its estimating higher light values than LAI-2000.

The means of estimated canopy openness values by spherical densiometer were also found to be higher (10.91%) than the DIFN mean values. CO may differ significantly from relative light intensity values, because the estimate is a structural parameter of the canopy and does not indicate light directly. During a gap study of Hungarian beech forests, CO values were also considerably higher than PACL values (calculated by tRAYci and from hemispherical photographs) both in gaps and under closed canopy conditions (Mihók et al. 2007).

Because of the overestimation of PACL and CO, DIFN is more appropriate for the absolute description of relative light intensity (similarly to direct methods), while CO and PACL can be used mainly for comparative studies (Comeau et al. 1998b, Gendron et al. 1998).

From the three methods, LAI-2000 and the tRAYci model proved to be more useful for investigating the relationship between the heterogeneity of light and understory vegetation in different forests than spherical densiometer. They gave relatively high correlation coefficients with each other and with the cover of blackberry at almost every scale, thus making studies of different spatial scales comparable.

Variation coefficient of LAI-2000 was higher than that of the other two methods, showing that this technique is more appropriate for detecting relative differences in light conditions. The LAI-2000's being one of the best methods is in agreement with other studies, often comparing different indirect methods to long-term absolute data collection (Comeau et al. 1998b, Gendron et al. 1998, Machado and Reich 1999, Engelbrecht and Herz 2001, Ferment et al. 2001, Rhoads et al. 2004). Measurements by LAI-2000 could have been more effective using a 180° or 90° view restrictor instead of a 270° one, but it requires repeated recordings in sample points increasing the time and cost of data collection (Gendron et al. 1998). Based on the high correlations of DIFN values with blackberry cover and with other methods, one record with a 270° view restrictor in each point is sufficient. An important advantage of the LAI-2000 device is that measurements can be taken even in deeply shaded stands, where e.g. the use of hemispherical photographs was not appropriate (Chazdon and Field 1987, Roxburgh and Kelly 1995, Machado and Reich 1999). However, according to other studies, under more open conditions, e.g. in gaps, LAI-2000 does not give reliable estimates. In these cases other methods such as light models, densiometer or fisheye photographs seem to be more favourable (Mihók et al. 2007).

TRAYci was not sensitive to the vertical placement of the points: neither the calculated PACL values, nor their correlations with blackberry cover differed significantly between measurements of 1.3 and 0.5 m height. Ferment et al. (2001), found that light measurements were more sensitive for vertical, than horizontal displacement in cases of spherical densiometer and hemispherical photographs. In our case, the weaker vertical sensitivity can be explained by the fact that canopy volume between 0.5 and 1.3 m height is negligible compared to canopy volume above 1.3 m. However, the increase of record number horizontally (from one to five per plot) resulted in considerably stronger correlations with blackberry cover, it was also modestly stronger than in the case of LAI-2000, at almost all spatial steps. These data show that tRAYci can give similar or better results than LAI-2000, but finding the best settings of tRAYci is not obvious. We could also construct relatively good models even if we used some simplifications: we did not make any measurements to estimate LAD of the species composing the vegetation and to quantify the thickness of the crown shell. Furthermore, during the crown radii measurements, the margin of the crown was estimated visually, and it was not measured by vertical mirror. Gersonde et al. (2004), also found that in the case of tRAYci, simplifications of crown representation showed little decline in model performance. As opposed to LAI-2000 and densiometer, an advantage of tRAYci is that calculating data in a finer resolution does not need additional field measurements. As opposed to the other two methods, tRAYci makes it also possible to calculate direct light, which also has an importance for the understory vegetation (Collins et al. 1985).

In all cases, the densiometer gave the weakest correlation coefficients with the cover of blackberry, but it showed significant correlations as well. The variation coefficient of CO values was the lowest, i.e. it is not able to sense the fine differences among points. This technique is based on estimation, so its results are not as reliable as the others' (Comeau et al. 1998b, Engelbrecht and Herz 2001, Ferment et al. 2001). However, it is a very simple, fast and inexpensive method, so it is favourable if many sampling sites have to be measured (Comeau et al. 1998b, Englund et al. 2000).

Data obtained by the densiometer could be more comparable if only one operator makes all the estimations (Comeau et al. 1998b).

We used the three methods to describe the light conditions in many different forest types. In this case time-consuming techniques could not be applied. Our results show that all three methods can be used with considerable simplifications of conditions to abridge fieldwork. Further practical aspects (cost, time requirement, etc.) in connection with the methods are discussed in many studies (Comeau et al. 1998b, Gendron et al. 1998, Engelbrecht and Herz 2001, Mihók et al. 2007).

We have to mention that reliability of each technique is largely dependent on the characteristics of the studied stands (light environments, heterogeneity, etc., Gendron et al. 1998). All of our sampling sites were in temperate mixed forests, but within this category we chose stands with various stand composition and structure. However, further comparisons are needed in other types of forests.

Effect of mean and heterogeneity of light

Heterogeneity of light (expressed by variation coefficient) showed much stronger correlations both between methods and a given method and blackberry cover than mean values. Among the studied forests, heterogeneity of light conditions differed more than the amount of light on the forest floor (which was relatively low in all cases). All of the stands had relatively closed canopy, but there were considerable structural differences among them. These differences were expressed more in the variation coefficients of light values causing stronger correlation values than mean.

In addition blackberry is a light flexible clonal plant with fast growing above-ground stems (Klimes et al. 1997). It can reach a relatively high cover at low stand level light intensity if there are at least some small brighter patches (Collins et al. 1985, Whigham 2004, Fotelli et al. 2005, Mountford et al. 2006). The studied stands had relatively closed upper canopy, therefore the effect of gaps in the heterogeneity of light is less important than the species composition of upper canopy and the presence or absence of shrub layer. Blackberry seemed to be sensitive for these fine spatial differences in understory light showing stronger relationships with light heterogeneity than amount.

Scales

The strength of correlations between different light estimating methods linearly increase with spatial steps having a maximum in most cases at the coarsest scale (30 x 30 m^2), in some cases at 20 x 20 m^2. It can be supposed that the more records are used for light estimation, the higher is the accuracy of the estimations and the similarity between the methods. At the scale of 5 x 5 m^2, none of the method-pairs correlated significantly. This scale (i.e. a single sampling point) proved not to be adequate to study the understory light environment. Because of methodological constrains, measurements in the same point with different techniques, were completed at different times. Small differences between the measurement positions can considerably influence the light estimations, because the canopy of the saplings can be very close to the devices. Neither model can give a reliable estimation about the light conditions of a single point, due to the simplifications of the crown structure. In addition, while the different view angle of the techniques influences light estimations in one point, this effect is less important when measuring more points in a grid. Based on our results, the used indirect techniques are more appropriate for the comparison of different forest stands than for detecting fine-scale light pattern within stands. This is in agreement with other methodological studies comparing these techniques both within and between forest stands (Engelbrecht and Herz 2001, Ferment et al. 2001).

The detected uni- and bimodal response to spatial scale of blackberry cover – light correlations cannot be explained by the increasing number of records and the accuracy of estimations. We may suppose that in the investigated forests the pattern of blackberry cover and light environment has the best fitting at intermediate (10 x 10 or 20 x 20 m^2) scale. As a light flexible plant, which is integrated by horizontal aboveground stolons, blackberry can respond to spatial heterogeneity of light mainly by the architectural modification of its patches (extension or senescence of ramets, Klimes et al. 1997). To investigate how the correlation of blackberry cover and light depends on spatial scale, we have to consider the scale-dependence of *Rubus* cover and light data, respectively.

The cover of blackberry (in percentage) increased with the size of the sampling unit until the scale of 15 x 15 m^2, after this scale, it does not change considerably (Fig. 1). The cover of *Rubus* in the stands was usually very low and it has an aggregated pattern. In a small sampling unit we had a small chance of finding any blackberry. However, increasing the sampling size (and the spatial scale), at some stands we could find more *Rubus*, so the mean and the standard deviation of the cover increased. As the cover did not change after 15 x 15 m^2, we can assume that the patches of the *Rubus* are smaller than this size, and above this scale its patches have a repeated pattern.

The heterogeneity of PACL, DIFN and CO showed a monotone increase with spatial steps (Fig. 1). Its cause may be that increasing sampling units, we could catch more and more closed or opened patches in the stand. These darker or brighter patches are caused by the heterogeneity of the crowns and the shrub layer, and this pattern could have a coarser scale than blackberry cover.

If we combine blackberry cover and light heterogeneity, we can investigate the dependence of the correlation coefficients on the spatial scale. If we take light data only from one point per plot, the coefficient of correlation reaches its maximum around 20 x 20 m^2 in the case of tRAYci, LAI-2000 and also densiometer (Fig. 1). It means that we can get the strongest correlation at a scale, which is slightly coarser than the pattern of blackberry patches. On the contrary, if we calculate light for five points per plot by tRAYci, we can get very strong correlations also under the scale of the *Rubus* patches (5 x 5 and 10 x 10 m^2). It is supposed that in this case we find information about the light in finer resolution, so it can better fit to the cover of *Rubus*.

Conclusions

LAI-2000 estimated the light conditions more correctly than the other two methods, which overestimated the relative light values. For comparison of different forest stands LAI-2000 and tRAYci were similarly appropriate, but the technical execution of the measurement was simpler by LAI-2000. In our case the heterogeneity of relative light resulted higher correlations than mean both between the different methods and between a method and blackberry cover.

The best scale to study the relationship between light and a light-flexible clonal plant, is dependent on the size of the patches of the plant. If we would like to get information at stand-level, e.g. to compare different forest types, investigations at coarser spatial scales exceeding the size of the plant patches are more appropriate. In these cases a lower spatial resolution of light measurements is sufficient. At the same resolution, there is no considerable difference between the tRAYci and LAI-2000, but from technical aspects, it is easiest to use the latter method. However, if our aim is to investigate the relationship between light and understory plants within a stand, we need a finer resolution of light measurement. We can get it easier by tRAYci, because this model can calculate light at any resolution without extra fieldwork.

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References

Anderson, M.C. 1964. Studies of the woodland light climate I. The photographic computation of light conditions. *Journal of Ecology* 52: 27-41.

Anderson, M.C. 1966. Stand structure and light penetration II. A theoretical analysis. *Journal of Applied Ecology* 3: 41-54.

Bellow, J.G. and P.K.R. Nair. 2003. Comparing common methods for assessing understory light availability in shaded-perennial agroforestry systems. *Agricultural and Forest Meteorology* 114: 197-211.

Brown, N., S. Jennings, P. Wheeler and J. Nabe-Nielsen. 2000. An improved method for the rapid assessment of forest understorey light environments. *Journal of Applied Ecology* 37: 1044-1053.

Brunner, A. 1998. A light model for spatially explicit forest stand models. *Forest Ecology and Management* 107: 19-46.

Brunner, A. 2004. *tRAYci - A light calculation program for spatially explicit forest stand models.* User's Manual, Danish Centre for Forest, Landscape and Planning, KLV, Hørsholm, Denmark

Brunner, A., D.B. Manning, J. Huss, D. Rozenbergar, J. Diaci, F. Schousboe and L.W. Hansen 2004. *Scenarios of regeneration and stand production of beech under different silvicultural regimes with Regenerator.* NAT-MAN Working Report 47.

Canham, C.D. and P.L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. In: Pickett, S.T.A. and P.S. White (eds.): *The ecology of natural disturbance and patch dynamics.* Academic Press Inc., Orlando. pp. 197-216.

Cescatti, A. 1997a. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithms. *Ecological Modelling* 101: 263-274.

Cescatti, A. 1997b. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. II. Model testing and application in a Norway spruce stand. *Ecological Modelling* 101: 275-284.

Chazdon, R.L. and C.B. Field. 1987. Photographic estimation of photosynthetically active Radiation - Evaluation of a computerized technique. *Oecologia* 73: 525-532.

Coates, K.D., C.D. Canham, M. Beaudet, D.L. Sachs and C. Messier. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *Forest Ecology and Management* 186: 297-310.

Collins, B.S., K.P. Dunne and S.T.A. Pickett. 1985. Responses of forest herbs to canopy gaps. In: Pickett, S.T.A. (ed.): *The ecology of natural disturbance and patch dynamics.* Academic Press Inc., London. pp. 218-234.

Comeau, P., R. Macdonald, R. Bryce and B. Groves. 1998a. *Lite: a model for estimating light interception and transmission through forest canopies, users manual and program documentation.* Research Branch, Ministry of Forests, Victoria, B.C. Working Paper 35/1998.

Comeau, P.G., F. Gendron and T. Letchford. 1998b. A comparison of several methods for estimating light under a paper birch mixedwood stands. *Canadian Journal of Forest Research* 28: 1843-1850.

Comeau, P.G. 2000. *Measuring light in the forest*. Extension Note 42, British Columbia Ministry of Forests, Victoria.

Comeau, P.G. and J.L. Heineman. 2003. Predicting understory light microclimate from stand parameters in young paper birch (*Betula papyrifera* Marsh.) stands. *Forest Ecology and Management* 180: 303-315.

Constabel, A.J. and V.J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. *Canadian Journal of Forest Research* 26: 1008-1014.

Emborg, J. 1998. Undestorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management* 106: 83-95.

Engelbrecht, B.M.J. and H.M. Herz. 2001. Evaluation of different methods to estimate understorey light conditions in tropical forests. *Journal of Tropical Ecology* 17: 207-224.

Englund, S.R., J.J. O'Brien and D.B. Clark. 2000. Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. *Canadian Journal of Forest Research* 30: 1999-2005.

Ferment, A., N. Picard, S. Gourlet-Fleury and Ch. Baraloto. 2001. A comparison of five indirect methods for characterizing the light environment in a tropical forest. *Annals of Forest Science* 58: 877-891.

Fotelli, M.N., P. Rudolph, H. Rennenberg and A. Gessler. 2005. Irradiance and temperature affect the competitive interference of blackberry on the physiology of European beech seedlings. *New Phytologist* 165: 453-462.

Frazer, G.W., R.A. Fournier, J.A. Trofymow and R.J. Hall. 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. *Agricultural and Forest Meteorology* 109: 249-263.

Gálhidy, L., B. Mihók, A. Hagyó, K. Rajkai and T. Standovár. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology* 183: 133-145.

Gendron, F., C. Messier and P.G. Comeau. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agricultural and Forest Meteorology* 92: 55-70.

Gersonde, R., J.J. Battles and K.L. O'Hara. 2004. Characterizing the light environment in Sierra Nevada mixed-conifer forests using a spatially explicit light model. *Canadian Journal of Forest Research* 34: 1332-1342.

Hale, S.E. and C. Edwards. 2002. Comparison of film and digital hemispherical photography across a wide range of canopy densities. *Agricultural and Forest Meteorology* 112: 51-56.

Hale, S.E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. *Forest Ecology and Management* 179: 341-349.

Jelaska, S.D., O. Antonic, M. Bozic, J. Krizan and V. Kusan. 2006. Responses of forest herbs to available understory light measured with hemispherical photographs in silver fir-beech forest in Croatia. *Ecological Modelling* 194: 209-218.

Ke, G. and M.J.A. Werger. 1999. Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. *Acta Oecologica* 20: 579-586.

Klimes, L., J. Klimesova, R. Hendriks and J. van Groenendael. 1997. Clonal plant architecture: a comparative analysis of form and function. In: de Kroon, H. and J. van Groenendael (eds.): *The ecology and evolution of clonal plants.* Backhuys, Leiden. pp. 1-29.

Lalic, B. and D.T. Mihailovic. 2004. An empirical relation describing leaf-area density inside the forest for environmental modeling. *Journal of Applied Meteorology* 43: 641-645.

Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2: 314-319.

Lemmon, P.E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* 55: 667-668.

LI-COR Inc. 1990. *LAI-2000 Plant Canopy Analyzer.* Instruction Manual. LI-COR Inc., Lincoln.

LI-COR Inc. 1991. *1000-90 Communication and utility software for LI-COR Instruments*. LI-COR Inc., Lincoln.

LI-COR Inc. 1992. *2000-90 Support software for the LAI-2000 Plant Canopy Analyzer*. LI-COR Inc., Lincoln.

MacFarlane, D.W., E.J. Green, A. Brunner and R.L. Amateis. 2003. Modeling loblolly pine canopy dynamics for a light capture model. *Forest Ecology and Management* 173: 145-168.

Machado, J.L. and P.B. Reich. 1999. Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. *Canadian Journal of Forest Research* 29: 1438-1444.

Marosi, S. and S. Somogyi (eds.) 1990. *Magyarország kistájainak katasztere. (Cadastre of Hungarian regions.)* MTA Földrajztudományi Kutató Intézet, Budapest.

Martens, S.N., D.D. Breshears and C.W. Meyer. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecological Modelling* 126: 79-93.

Matthews, J.D. 1991. *Silvicultural Systems*. Calderon Press, Oxford.

Messier, C. and P. Puttonen. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands - the basis for a quick and efficient method of characterizing light. *Canadian Journal of Forest Research* 25: 343-354.

Messier, C. and S. Parent. 1997. Reply - The effects of direct-beam light on overcast day estimates of light availability: On the accuracy of the instantaneous one-point overcast-sky conditions method to estimate mean daily %PPFD under heterogeneous overstory canopy conditions. *Canadian Journal of Forest Research* 27: 274-275.

Messier, C., S. Parent and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9: 511-520.

Mihók, B. and T. Standovár. 2005. *Fénybecslési módszerek összehasonlító vizsgálata az Ipoly Erdő Rt. Királyréti Erdészete által bükkös állományokban létesített mesterséges lékekben. (Comparison of light estimating methods in artificial gaps of beech forest made by the Ipoly Erdő Rt., Forestry of Királyrét.)* Working report, Királyrét, Hungary.

Mihók, B., A. Hagyó, T. Standovár, L. Gálhidy and J. Ruff. 2007. Figyeljük a fény játékát - Milyen módszert használjunk erdei állományokban kialakuló lékek fényviszonyainak jellemzésére? (What is the appropriate method to describe the light conditions of forest gaps?) *Erdészeti Lapok* 142: 156-159.

Mizunaga, H. 2000. Prediction of PPFD variance at forest floor in a thinned Japanese cypress plantation. *Forest Ecology and Management* 126: 309-319.

Mountford, E.P., P.S. Savill and D.P. Bebber. 2006. Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. *Forestry* 79: 389-408.

Parent, S. and C. Messier. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Canadian Journal of Forest Research* 26: 151-154.

Pinno, B.D., V.J. Lieffers and K.J. Stadt. 2001. Measuring and modelling the crown and light transmission characteristics of juvenile aspen. *Canadian Journal of Forest Research* 31: 1930-1939.

Rhoads, A.G., S.P. Hamburg, T.J. Fahey, T.G. Siccama and R. Kobe. 2004. Comparing direct and indirect methods of assessing canopy structure in a northern hardwood forest. *Canadian Journal of Forest Research* 34: 584-591.

Roxburgh, J.R. and D. Kelly. 1995. Uses and limitations of hemispherical photography for estimating forest light environments. *New Zealand Journal of Ecology* 19: 213-217.

Silbernagel, J. and M. Moeur. 2001. Modeling canopy openness and understory gap patterns based on image analysis and mapped tree data. *Forest Ecology and Management* 149: 217-233.

SPSS Inc. 2005. *SPSS 14.0 for Windows. Release 14.0.0*. SPSS Inc.

Stadt, K.J., S.M. Landhausser and J.D. Stewart. 1997. Comment - The effects of direct-beam light on overcast day estimates of light availability. *Canadian Journal of Forest Research* 27: 272-274.

Stadt, K.J. and V.J. Lieffers. 2000. MIXLIGHT: a flexible light transmission model for mixed-species forest stands. *Agricultural and Forest Meteorology* 102: 235-252.

Tímár, G., P. Ódor and L. Bodonczi. 2002. Az Őrségi Tájvédelmi Körzet erdeinek jellemzése. (The characteristics of forest vegetation of the Őrség Landscape Protected Area.) *Kanitzia* 10: 109-136.

Tinya, F., S. Márialigeti, I. Király, B. Németh, P. Ódor. in press. The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, Western Hungary. *Plant Ecology*.

Tutin, T.G., V.H. Heywood, N.A. Burges, D.M. Moore, D.H. Valentine, S.M. Walters and D.A. Webb. 1964-1993. *Flora Europea*. Cambridge University Press, Cambridge.

Valladares, F. and B. Guzman. 2006. Canopy structure and spatial heterogeneity of understory light in an abandoned Holm oak woodland. *Annals of Forest Science* 63: 749-761.

Welles, J.M. 1990. 3. Some indirect methods of estimating canopy structure. *Remote Sensing Reviews* 5: 31-43.

Welles, J.M. and J.M. Norman. 1991. Instrument for indirect measurement of canopy architecture. *Agronomy Journal* 83: 818-825.

West, D.C., H.H. Shugart and D.B. Botkin. 1981. *Forest succession. Concepts and application.* Springer Verlag, New York.

Whigham, D.F. 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology Evolution and Systematics* 35: 583-621.

Zar, J.H. 1999. *Biostatistical analysis*. Prentice Hall, New Jersey.

Tables

Table 1. Data on stand structure, light variables and cover of *Rubus fruticosus agg.* in the selected forest stands. DIFN: diffuse non-interceptance measured by LAI-2000; CO: canopy openness estimated by spherical densiometer; PACL: percentage of above canopy light calculated by tRAYci model at 1.3 m height. Stand structural data are based on 40 x 40 m^2 sized blocks, light variables and blackberry cover (mean ± standard deviation) are based on 36 plots of 5 x 5 m^2 size.

ID	Number of trees per ha	Number of tree species	Relative number of oaks	Relative number of beech and hornbeam	Relative number of pine and spruce	Mean height of dominant trees (m)	Total volume of trees (m^3/ha)	DIFN (%)	DIFN (%) coefficient of variation	CO (%)	CO (%) coefficient of variation	PACL (%)	PACL (%) coefficient of variation	Blackberry cover (% of the ground area)
099	287.5	6	0.61	0.28	0.00	23.4	376.5	7.76 ± 3.64	0.47	17.14 ± 6.84	0.40	20.56 ± 70	0.34	3.04 ± 2.75
101	581.3	7	0.02	0.46	0.41	23.1	309.9	5.55 ± 4.05	0.73	8.98 ± 5.24	0.58	8.30 ± 4.31	0.52	0.13 ± 0.29
102	787.5	9	0.21	0.35	0.35	22.0	340.8	1.20 ± 0.95	0.79	5.14 ± 1.67	0.32	7.76 ± 3.17	0.41	0.14 ± 0.23
107	775.0	5	0.10	0.76	0.10	19.4	264.2	1.90 ± 1.72	0.90	9.46 ± 3.72	0.39	6.42 ± 1.81	0.28	0.13 ± 0.46
108	693.8	5	0.17	0.28	0.53	19.0	288.5	6.03 ± 4.43	0.74	15.15 ± 6.04	0.40	27.66 ± 7.93	0.29	0.00 ± 0.00
111	331.3	5	0.06	0.85	0.08	25.4	419.0	1.66 ± 0.36	0.22	5.52 ± 0.99	0.18	7.86 ± 1.00	0.13	0.02 ± 0.04
116	318.8	4	0.20	0.78	0.02	28.3	544.6	1.70 ± 0.43	0.25	11.30 ± 2.27	0.20	8.14 ± 1.31	0.16	0.28 ± 0.64
117	306.3	5	0.22	0.41	0.37	26.0	461.9	3.34 ± 0.88	0.26	8.04 ± 1.39	0.17	17.95 ± 1.80	0.10	0.02 ± 0.07
118	425.0	4	0.07	0.57	0.35	30.0	617.2	1.68 ± 0.32	0.19	19.91 ± 4.24	0.21	14.4 ± 1.92	0.13	0.00 ± 0.00
121	1181.3	6	0.03	0.55	0.34	21.5	518.5	1.23 ± 0.37	0.31	5.50 ± 1.14	0.21	8.70 ± 1.90	0.22	0.02 ± 0.05
126	456.3	4	0.21	0.37	0.42	25.5	364.9	6.04 ± 4.00	0.66	22.43 ± 5.18	0.23	34.76 ± 14.2	0.41	5.55 ± 7.28
129	356.3	6	0.44	0.44	0.10	24.3	484.6	4.13 ± 1.84	0.45	5.36 ± 1.76	0.33	27.78 ± 6.97	0.25	0.09 ± 0.19
130	537.5	8	0.30	0.56	0.01	23.5	402.2	1.51 ± 1.15	0.76	8.61 ± 2.02	0.24	11.61 ± 4.27	0.37	0.25 ± 0.53
131	687.5	6	0.31	0.49	0.18	23.6	534.5	1.64 ± 1.02	0.62	11.37 ± 4.14	0.36	14.42 ± 3.95	0.27	0.04 ± 0.08
132	406.3	5	0.38	0.51	0.09	24.6	449.8	2.32 ± 1.32	0.57	7.41 ± 1.80	0.24	8.82 ± 3.32	0.38	0.41 ± 2.33
136	300.0	4	0.17	0.77	0.06	31.6	567.8	3.50 ± 1.10	0.31	11.70 ± 2.22	0.19	23.96 ± 3.01	0.13	0.05 ± 0.16
138	487.5	8	0.55	0.22	0.18	26.5	560.7	3.27 ± 2.05	0.63	15.65 ± 5.39	0.34	27.23 ± 6.12	0.22	0.24 ± 0.60
142	500.0	7	0.03	0.54	0.41	30.8	576.8	1.63 ± 1.14	0.70	9.63 ± 3.01	0.31	5.65 ± 2.35	0.42	0.68 ± 1.33
151	725.0	7	0.05	0.81	0.12	19.7	278.3	1.18 ± 0.52	0.44	8.83 ± 2.28	0.26	7.47 ± 1.76	0.24	0.04 ± 0.17
152	418.8	6	0.06	0.54	0.37	30.5	633.8	1.26 ± 0.48	0.38	16.10 ± 2.94	0.18	11.62 ± 1.66	0.14	0.01 ± 0.02
156	1112.5	8	0.08	0.24	0.41	22.0	419.1	1.64 ± 2.02	1.23	10.58 ± 5.74	0.54	8.85 ± 4.41	0.50	0.05 ± 0.09
158	506.3	4	0.22	0.49	0.28	29.0	615.1	2.22 ± 0.53	0.24	10.58 ± 1.94	0.18	7.69 ± 1.87	0.24	0.00 ± 0.00
160	806.3	4	0.05	0.63	0.32	24.7	494.2	0.91 ± 0.30	0.33	6.51 ± 1.38	0.21	8.48 ± 1.87	0.22	0.00 ± 0.00
Mean								2.75	0.53	10.91	0.29	14.18	0.28	0.49

Table 2. The used leaf area density (LAD, m^2/m^3) parameters of the main overstory trees and species of shrub layer for the tRAYci model.

Species	LAD (m^2/m^3)	
	Overstory	Shrub layer
Betula pendula	0.10	0.10
Carpinus betulus	2.00	
Corylus avellana	0.40	0.40
Fagus sylvatica	2.00	0.40
Frangula alnus		0.40
Picea abies	0.45	0.27
Pinus sylvestris	0.10	
Quercus petraea	0.25	0.10
Quercus robur	0.25	
Quercus rubra	2.00	
Tilia cordata	2.00	0.40

Table 3. Spearman correlation coefficients and their significance among variables of light estimated by different methods in five spatial scales and expressed as mean and coefficient of variation. n=23. DIFN: diffuse non-interceptance measured by LAI-2000; CO: canopy openness estimated by spherical densiometer; PACL: percentage of above canopy light calculated by tRAYci model at 1.3 m height; *: $p<0.05$; **: $p<0.01$.

	5x5 m	10x10 m	15x15 m	20x20 m	30x30 m
			mean		
DIFN – CO	0.240	0.196	0.328	0.275	0.423*
PACL – DIFN	-	0.282	0.469*	0.574*	0.588*
PACL – CO	0.333	0.453*	0.465*	0.418*	0.432*
			coefficient of variation		
DIFN – CO	-	0.754*	0.771*	0.788*	0.773*
PACL – DIFN	-	0.488*	0.717*	0.831*	0.824*
PACL – CO	-	0.451*	0.670*	0.748*	0.751*

Table 4. Spearman correlation coefficients and their significance between the cover of *Rubus fruticosus agg.* and the different variables of light studied at five different scales and expressed as mean and coefficient of variation. n=23. PACL: percentage of above canopy light calculated by tRAYci model at 1.3 and 0.5 m height, "–5" means calculation at 5 points per plot; DIFN: diffuse non-interceptance measured by LAI-2000; CO: canopy openness estimated by spherical densiometer; *: p<0.05; **: p<0.01.

	5 x 5 m	10 x 10 m	15 x 15 m	20 x 20 m	30 x 30 m
			mean		
PACL 1.3	-	-0.083	0.246	0.154	0.051
PACL 0.5	-	-0.083	0.214	0.126	0.027
PACL 0.5 – 5	-	-0.146	0.209	0.121	0.051
DIFN	0.153	0.272	0.408	0.390	0.307
CO	0.090	-0.051	0.015	0.070	0.083
			coefficient of variation		
PACL 1.3	-	0.471*	0.479*	0.518*	0.545**
PACL 0.5	-	0.458*	0.441*	0.507*	0.535**
PACL 0.5 – 5	0.667	0.696**	0.459*	0.578**	0.574**
DIFN	-	0.413	0.512*	0.537**	0.486*
CO	-	0.233	0.425*	0.457*	0.369

Figure captions

Fig. 1. Cover of *Rubus fruticosus agg.* (in %, diamonds), variation coefficient of light variables (squares) and its correlation coefficients with *Rubus* cover (triangles) plotted against the spatial scales. a) Percentage of above canopy diffuse light (PACL) values calculated by tRAYci model at 0.5 height for one point per plot. b) Percentage of above canopy diffuse light (PACL) values calculated by tRAYci model at 0.5 height for five point per plot. c) Diffuse non-interceptance (DIFN) values measured by LAI-2000. d) Canopy openness (CO) estimated by spherical densiometer.

Figures

Fig.1.