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Temporal variations in the understorey photosynthetic photon flux density of a deciduous stand: the effects of canopy development, solar elevation, and sky conditions

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Abstract

The effects of canopy development, solar elevation, and sky conditions on temporal variation in photosynthetic photon flux density (PPFD) were examined within a 9-year-old bigleaf maple stand on Vancouver Island (Canada). PPFD was measured every second and stored as 10-min averages from 18 May to 14 October 1996, at 52 microsites characterised according to their growing season %PPFD (GSP). PPFD and %PPFD variability was examined at three different temporal levels. Specific days in May, July, and September with clear and overcast sky conditions were selected to separate the effects of canopy development and solar elevation on diurnal and seasonal light variability.

Diurnal light variability expressed as the mean of the difference between two consecutive 10-min averages of PPFD and %PPFD decreased with increasing GSP on clear days in May. For clear days in July and September, variability was characterised by arc-shaped relationships with high variability for microsites receiving between 20 and 80% GSP and lower variability for microsites below 20 and above 80% GSP. On overcast days, diurnal variability in PPFD increased with increasing GSP while diurnal variability in %PPFD showed an arc-shape relationship. The coefficient of variation of PPFD and %PPFD decreased with increasing GSP on clear days and sunflecks decreased with decreasing GSP and from May to September.

Day-to-day light variability expressed as the mean difference between consecutive daily PPFD increased with increasing GSP while the mean difference between consecutive daily %PPFD was higher for microsites receiving between 20 and 80% GSP. The coefficient of variation for the daily PPFD and %PPFD was higher for microsites receiving <20% GSP compared to other microsites.

Seasonal light variability showed that microsites with <50% GSP received up to eight times more light in May than in July on both clear and overcast sky conditions because of canopy development. From July to September in clear sky conditions, decrease in light was variable for microsites receiving <40% GSP; probably because of the position of microsites in relation

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to the solar track. On overcast days, mean daily PPFD above canopy and in the understorey was 2 to 3 times higher in July than in September while mean daily %PPFD remained stable.

The possible effects of the types of diurnal and day-to-day light variability on physiological and morphological responses of understorey plants are discussed.

Keywords: Deciduous forest; Light penetration; Phenology; Photon flux density; Sun angle; Temporal light variability

1. Introduction

Although light availability is generally considered as one of the factors having the greatest impact on plant growth performance, recent work has shown that temporal variations in light may also have a significant impact on plant growth (Wayne and Bazzaz, 1993; Ackerly, 1997; Robison and McCarthy, 1999). Most studies on light variability have characterised plant growth under experimentally-controlled conditions (e.g. Wayne and Bazzaz, 1993; Yanhong et al., 1994; Robison and McCarthy, 1999). This approach reduces problems introduced by other variables and facilitates the detection of plant growth differences attributable to variability in light among treatments. However, light is highly variable both spatially and temporally under conditions of direct light in natural environments (Baldocchi and Collineau, 1994). Light availability and variability at various microsites beneath the forest understorey is influenced by leaf phenology, position of the solar track, sky conditions, location within gaps, gap size, and canopy height (Anderson, 1970; Canham et al., 1990; Baldocchi and Collineau, 1994). As a first step towards understanding the potential influence of temporal fluctuations in light on plant growth, it is necessary to characterise this variation.

Long-term monitoring of light in the forest understorey at very short time steps has been rarely done because of the cost of sensors and data-loggers, and the large amount of time required for the frequent downloading and maintenance of instruments. In the earliest studies, light climate in forests was generally described in terms of daily light totals (Anderson, 1964) and measured as solar irradiance (300–3000 nm, Anderson, 1964; Hutchison and Matt, 1977). In recent years, new equipment has become available for measuring and recording frequent light measurements in order to detect short-term light variations in the understorey. This equipment also permits the collection of data over long periods of time for large numbers of microsites in the spectral range usable by plants (i.e. the photosynthetic photon flux density: PPFD, 400–700 nm). Ideally, the best method to characterise the variability of light regimes in the forest understorey involves continuous measurement of light over one or more growing seasons at numerous sampling points in order to sample a range of canopy development and sky conditions. However, this has rarely been done in forest ecosystems. One limitation that is common to most studies is in the frequency of light measurements since light was not measured continuously, but at specific periods during the growing season (e.g. Baldocchi et al., 1984, 1986; Ross et al., 1986; Constabel and Lieffers, 1996). Another limitation is the small number of microsites sampled. For example, light was characterised in only a few contrasting light environments such as in closed-canopy microsites and gaps (e.g. Chazdon and Fetcher, 1984; Chazdon, 1986; Turnbull and Yates, 1993) or as stand-level averages (e.g. Ross et al., 1986; Constabel and Lieffers, 1996; Roujean, 1999). Finally, many studies were done under only one sky condition, that being mostly clear sky conditions (e.g., Baldocchi et al., 1984, 1986; Ross et al., 1986; Constabel and Lieffers, 1996). Hence, there appears to be no comprehensive study of light variability under a wide range of canopy and sky conditions in a deciduous forest throughout the whole growing season. In contrast to coniferous forests, deciduous forests exhibit marked seasonal light variability and this is known to influence understorey plant growth.

The aim of this article is to characterise the effects of canopy development, solar elevation, and sky conditions on the temporal variation in light for a wide range of understorey microsites in a deciduous forest. Light was measured every second and stored as 10-min averages from May to October at 52 microsites in the understorey of a young bigleaf maple stand that represented the whole range of light transmission over a growing season. The originality of this study was to evaluate light variability at three different levels: diurnal, day-to-day, and seasonal light variability. The effect of light variability on plant growth depends on the level of variability and on the response time of traits in plants. Ackerly (1997) demonstrated that different plant traits are influenced by different levels of light variability. To characterise the diurnal and seasonal light variability, representative days in May, July, and September were selected to determine the effects of canopy development from May to July and changes in solar elevation from July to September for both clear and overcast sky conditions. In addition, the potential implications of diurnal and day-to-day light variability on plant growth are discussed.

2. Methods

2.1. Study site

The study was conducted on a site located ≈13 km northeast of Port Alberni (49°N, 125°W) on Vancouver Island in British Columbia, Canada, during the summer of 1996. The site consisted of 9-year-old bigleaf maple (*Acer macrophyllum* Pursh.) clumps that have resprouted following clearcutting in 1988 (Thomas and Comeau, 1998). Before the clearcut, the site was dominated by Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and bigleaf maple. In April 1996, six 30 m×30 m plots were established to provide a wide range of maple densities and light conditions. Maple density ranged from 0 to 400 clumps per hectare, average height of clumps was about 9.3 m, and mean crown radius of clumps ranged from 237 to 273 cm per plot. The study site is described in more detail by Gendron et al. (1998). Leaf area index (LAI) was assessed using an LAI-2000 (LI-COR, Lincoln, NE) in May and July 1996.

2.2. Light measurements

A systematic grid of 25 points (6 m spacing between points) was established in each plot, and of these, 10 were randomly selected for installation of photodiodes 2 m above the ground to measure PPFD. Gallium arsenide phosphide photodiodes (Hamamatsu, model G2711-01, Middlesex, NJ) were chosen because of their low cost and good spectral response between 300 and 680 nm (Pearcy, 1989; Pontailler, 1990). The spectral response curve can be found in Pontailler (1990). Levelled photodiodes were connected to a CR-10 data-logger (Campbell Scientific, Logan, UT) installed in the middle of each plot. Photodiodes were calibrated against quantum sensors (model LI-190SA, LI-COR, Lincoln, NE) in both early and late summer. A complete description of the calibration can be found in Gendron et al. (1998). A quantum sensor (LI-190SA, LI-COR, Lincoln, NE) was installed at the top of a nearby 13-m tree and connected to a CR-10 data-logger to record above-canopy light. Below- and above-canopy PPFD were measured every second and stored as 10-min averages to reduce the quantity of data while maintaining a sufficiently short time interval to detect short-term variability in light conditions (Chazdon and Fetcher, 1984; Turnbull and Yates, 1993). Continuous measurements were recorded from 18 May to 14 October 1996 between 0400 and 2100h (Pacific Time Zone) at the beginning of the summer and between 0600 and 1800h at the end of the summer. The sum of below-canopy PPFD recorded by each photodiode was divided by the sum of above-canopy PPFD to calculate the measured %PPFD for each photodiode location. Since the measured %PPFD was calculated from continuous measurements during 5 months in the growing part of the year, it will be referred to as growing season %PPFD (GSP) hereafter. A total of 52 photodiodes were used in this study and each photodiode microsite will be identified as its GSP.

2.3. Light variability

Ten-minute averages recorded by the data-loggers from 0600 to 1800 h were used in the calculations. This sampling period was chosen so that every selected day had the same number of 10-min averages over the whole growing season. Light variability was categorised at three levels as diurnal, day-to-day, and seasonal light variabilities. Plant traits respond differently to various levels and types of light variability and their response is often related to plant growth rates and leaf life span (Ackerly, 1997). Consequently, two types of light variability were calculated as the mean of the differences between two consecutive 10-min averages or days and the coefficient of variation (CV) for diurnal and day-to-day light variability. The mean of the differences between two consecutive 10-min averages or days is a new way to characterise light variability and measures the absolute difference between consecutive light readings. Its originality lies in that it characterises the temporal sequence of light variability. It is a fine-grained light variability since it takes into account the temporal sequence of light readings. On the other hand, the CV is more commonly used to characterise light variability (e.g. Chazdon and Fetcher, 1984; Baldocchi et al., 1986; Wayne and Bazzaz, 1993). Unlike the difference between consecutive light reading, it does not take into account the temporal sequence of light readings. CV was calculated as the standard deviation expressed as a percentage of the mean. Consequently, the CV has the advantage of comparing light variability independently of the magnitude of their means.

2.3.1. Diurnal light variability

Mean of the absolute difference between two consecutive 10-min averages of PPFD and between two consecutive 10-min averages of %PPFD were calculated on a few representative selected days. It is a fine-grained light variability since it takes into account how light fluctuates from one 10-min average to the next within a day. Such light variability may elicit physiological change in traits with relatively rapid response times, such as stomatal responses, conductance, and photosynthetic induction (Ackerly, 1997). Light was considered more variable when there were large fluctuations between two consecutive 10-min averages. The difference was calculated for each photodiode on two consecutive 10-min averages expressed as absolute values (μmol m^{-2} s^{-1}) and %PPFD for the six selected days. Days were selected at the beginning, the middle, and the end of the growing season on both clear and overcast sky conditions (Table 1) to separate the effects of canopy development and solar elevation on incoming PPFD. Accordingly, days in May and in July were selected about 28 days before and after the summer solstice. Solar elevation was similar for these selected days, but canopy cover was different since the bigleaf maple canopy was still developing during May. Days in July and September had different solar elevations, but similar canopy cover since bigleaf maple loses its leaves in October and November. Clear and overcast days were selected within each of these three periods. Completely clear and overcast days were selected to isolate the effect of the sun or clouds on light variability. Days with mixed sky conditions were not selected since it is not possible to consider separately the effects of canopy gaps and broken clouds. Thus, on clear days light variability was influenced by direct and diffuse light. On the other hand, light variability on overcast days was influenced by diffuse light since the solar disk was not visible. In order to characterise sky conditions, above-canopy PPFD was illustrated by data sampled by the quantum sensor in the open at 10-min intervals throughout the course of the day. Days with clear sky conditions were selected when changes in above-canopy PPFD measured over the course of the day were illustrated by the characteristic concave down hyperbola shape, indicating the absence of clouds. On days with overcast sky conditions, the density of cloud cover was sufficiently high to reduce incident direct beam flux densities to very low (nearly all 10-min averages were <900 μmol m^{-2} s^{-1}) and fairly stable PPFD values (Table 1). In overcast sky conditions, the PPFD was reduced to very low light level and was composed of diffuse light.

Table 1
Characteristics of the above-canopy PPFD on the six selected days during the growing season

Period	Sky condition	Date and Julian day	Solar elevation (degrees)	Mean daily PPFD (μmol m^{-2} s^{-1}) ($\pm$s.e.)
Beginning	Clear	May 26 (147)	62.1	1263.35 (56.22)
	Overcast	May 20 (141)	60.9	418.11 (25.65)
Middle	Clear	July 14 (196)	62.5	1292.49 (56.52)
	Overcast	July 19 (201)	61.5	419.69 (37.28)
End	Clear	Sep 10 (254)	44.8	836.51 (60.37)
	Overcast	Sep 6 (250)	46.3	167.38 (11.15)

The coefficient of variation (CV) of the 10-min averages of PPFD and %PPFD was calculated on the selected days. Light was considered variable when CV was large. This is a coarse-grained type of light variability since it measures the relative light variability within a day. It will be referred to as CV_w hereafter.

The daily frequency in percentage of individual sunfleck events >250 μmol m^{-2} s^{-1} (Messier et al., 1998) and their relative contribution to daily PPFD in percentage were also examined for all 52 microsites on the selected days in clear sky conditions. The calculations were done using light readings recorded from 06:00 to 19:00 h. This sampling period is longer than the one described above, because photodiodes received PPFD later in the evening under clear sky conditions compared to overcast days. Sunflecks are a short-term elevation of PPFD that usually last from a few seconds to <10 min (Canham et al., 1990; Baldocchi and Collineau, 1994; Messier et al., 1998). Consequently, averaging light over a 10-min period may obscure some of the sunfleck activity. However, this approach provides an estimation of light penetration to the understorey.

2.3.2. Day-to-day light variability over the growing season

The mean difference between consecutive daily PPFD and daily %PPFD was calculated for the period from 18 May to 14 October. The difference between daily PPFD and %PPFD for consecutive days describes the temporal variation in light from one day to the next over the growing season. This provides a fine-grained measurement of light variability. Physiological traits influenced by day-to-day changes in light such as photosynthetic capacity and photoperiodic responses are likely to respond to this frequency of variation in light conditions (Ackerly, 1997). However, few morphological traits have sufficiently rapid response times to track day-to-day light variability (Ackerly, 1997). Large differences between consecutive daily PPFD and daily %PPFD were considered to indicate high levels of day-to-day variability.

CV was calculated for the daily PPFD and daily %PPFD from 18 May to 14 October. Variability was considered to be high when the CV was large. This statistic provides a measurement of coarse-grained light variability, since it measures the relative daily light variability throughout the growing season. This type of light variability will be referred to as CV_d hereafter.

2.3.3. Seasonal light variability

The ratio between May and July measurements of mean daily PPFD and mean daily %PPFD was calculated to describe the effect of canopy development on seasonal variability in understorey light. In addition, the ratio between July and September measurements of mean daily PPFD and mean daily %PPFD was calculated to evaluate the effect of solar elevation on seasonal light variability. The ratios were calculated using the same selected clear and overcast days used to describe variation in diurnal light. Seasonal light variability may elicit changes in traits such as photosynthetic acclimation, leaf morphology, plant growth, and growth allocation (Ackerly, 1997).

2.4. Statistical analysis

Linear regression analysis was used to examine the relationships between the different measures of light variability and GSP. If the relationship was nonlinear, appropriate transformations were applied to convert the relationship to a linear form (Sit and Poulin-Costello, 1994). However, certain relationships in day-to-day and seasonal light variabilities could not be explained by any linear regression because linearity and homoscedasticity could not be achieved. In the relationships between the relative contribution to daily PPFD and GSP, we used the natural growth equation $Y=a(1-\exp(-bx))$. In the natural growth equation, the asymptote a was defined as 100.1% since many microsites had a relative contribution of sunflecks equal to 100%. Covariance analysis was used to determine if there were seasonal differences in:

1. the mean of the difference between two consecutive 10-min averages of PPFD and %PPFD;
2. the coefficient of variation (CV_w) of the 10-min averages of PPFD and %PPFD; and
3. frequency of sunflecks.

Covariance analysis was performed separately for data from clear and overcast days using selected days in July. For this analysis, day was used as a main effect and GSP as a covariate. To adjust the model for departure from linearity of the relationship, the square term of the covariate was used. All analysis were performed using the SAS statistical package for

Windows (V. 6.12; SAS Institute Inc., Cary, NC). We present the results for the untransformed data.

3. Results and discussion

Growing season %PPFD for the 52 understorey microsites ranged from 4.7 to 97.7 %PPFD. In May, LAI ranged from 0.33 to 0.96 $m^2 m^{-2}$ in the six plots. There was a large increase in canopy development at the end of the spring and beginning of the summer since LAI in July was generally more than three times higher than in May, ranging from 0.59 to 3.03 $m^2 m^{-2}$ in the six plots.

3.1. Diurnal light variability

On clear days in May, the mean of the differences between two consecutive 10-min averages of PPFD and %PPFD decreased, starting at 30% GSP as GSP increased (Fig. 1A and D). Low light microsites probably did not receive sunlight continuously during the day in May, because of the presence of dense maple clumps, so variability was high. In July and September, variability was characterised by arc-shaped relationships with high variability for microsites receiving between 20 and 80% GSP and lower variability for microsites at both low and high levels of GSP (Fig. 1B, C, E, F). Direct light penetration is influenced by the interplay between canopy gaps and position of the solar disk (Rich et al., 1993), and it could be responsible for the high light variability observed between 20 and 80% GSP where gaps are found. Microsites receiving >80% GSP were generally characterised by low light variability on clear days since light was received continuously without being intercepted by vegetation.

The decline in solar elevation from July to September did not appear to affect light variability on clear days, since the mean of the difference between two consecutive 10-min averages of PPFD and %PPFD were not significantly different between July and September in the young maple canopy. However, Ross et al. (1986) reported that light under boreal deciduous forests was more variable in July than in September because of the lower solar elevation and less direct light in September. Their sampling may have underestimated light variability in September since the selected day at this period was cloudy and measurements were only taken between 1100h and 1500h to minimise diurnal solar track variation.

On overcast days, the mean of the difference between two consecutive 10-min averages of PPFD increased with GSP in the three selected days during the growing season (Fig. 1G–I). Unlike direct light that originates from the sun, diffuse light produced on cloudy days originates from all parts of the sky and its penetration to the understorey is influenced more by the amount of canopy openings or gap fraction than by the location of the gaps relative to the sun. Hence, large differences from one 10-min average to the next in above-canopy light variability caused by the rapid change in cloud density resulted in proportionally larger differences from one 10-min average to the next for microsites with high GSP (up to 110 $\mu mol\, m^{-2} s^{-1}$) than for microsites with low GSP. Here, the absolute change in PPFD from one 10 min to the next is directly related to the absolute PPFD value and to the above-canopy light variability. Conversely, since little PPFD reached low GSP microsites, the difference between consecutive 10-min averages were low in absolute values. The above-canopy light variability was buffered by the vegetation in low light microsites.

On overcast days, the mean of the difference between two consecutive 10-min averages of %PPFD was characterised by an arc-shaped relationship with higher variability for microsites receiving between 40 and 80% GSP and lower variability for microsites at both low and high levels of GSP (Fig. 1J–L). This arc-shaped relationship for %PPFD is hard to explain. Light variability was very low (<5%) for all microsites in May, July, and September. Temporal stability in %PPFD on overcast days was also characterised by Messier and Puttonen (1995) who reported that the 5-min averages of %PPFD were fairly constant throughout overcast days under Scots pine stands.

CV_W of the 10-min averages of PPFD and %PPFD on selected days was also calculated to characterise diurnal light variability. On clear days, CV_w decreased with increasing GSP (Fig. 2A–F). CV_w calculated using 10-min averages of %PPFD on clear days in July ranged from 100 to 200% for low GSP microsites. This corresponds to the CV of 166% calculated by Baldocchi et al. (1986) beneath a *Quercus–Carya* forest on clear sky conditions in July. They also showed that CV decreased from 166 to 20% with increasing height

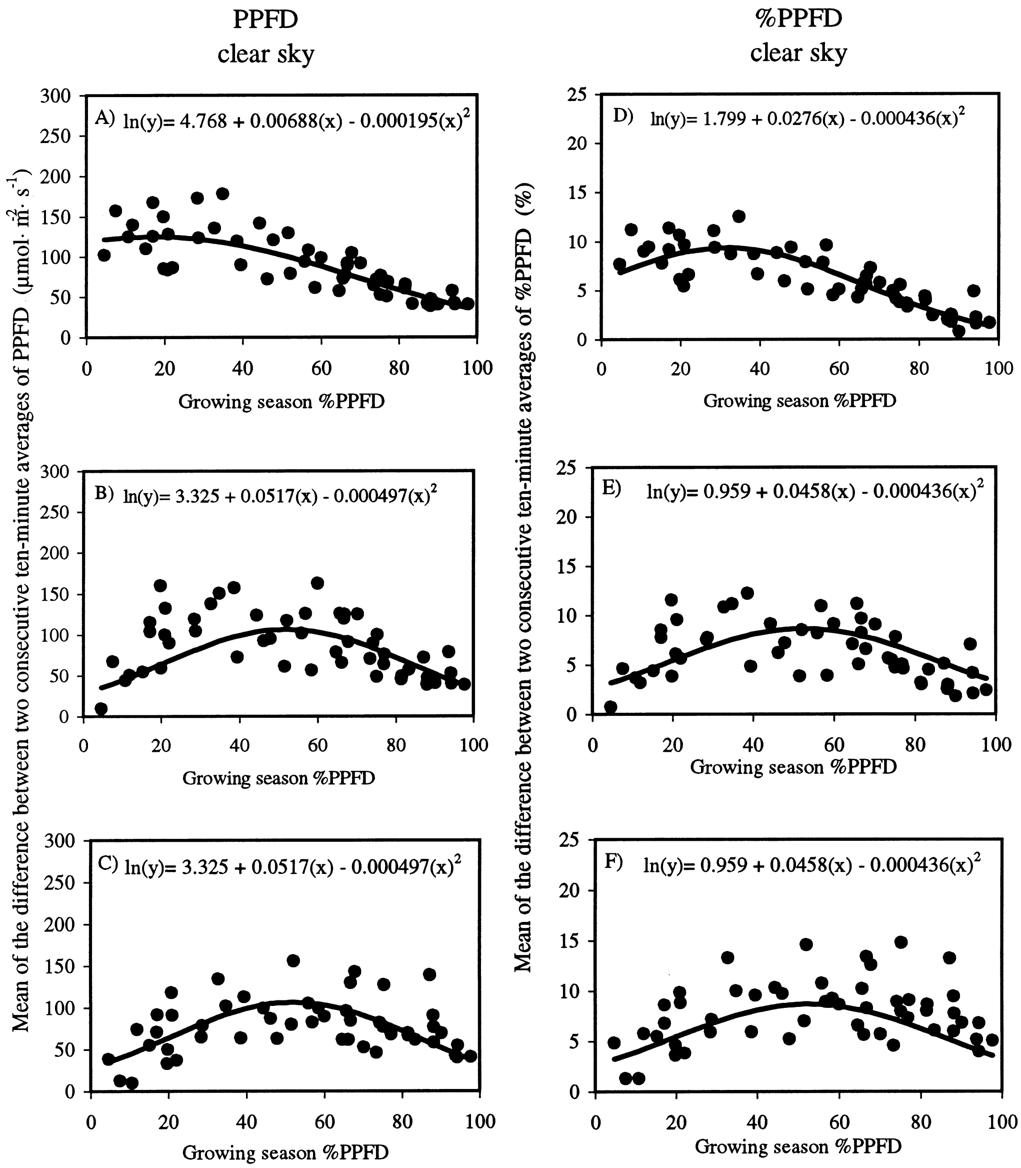


Fig. 1. Mean of the difference between two consecutive 10-min averages of PPFD and %PPFD in May (A, D, G, J), July (B, E, H, K), and September (C, F, I, L) under clear and overcast sky conditions for understorey microsites ranging from 4.7 to 97.7% growing season PPFD. Relationships were calculated from covariance analysis. R^2 and probabilities of the models are as follows: mean of the difference between two consecutive 10-min averages of PPFD on clear days: r^2=0.48 and p<0.001, mean of the difference between two consecutive 10-min averages of %PPFD on clear days: r^2=0.50 and p<0.001, mean of the difference between two consecutive 10-min averages of PPFD on overcast days: r^2=0.97 and p<0.001, and mean of the difference between two consecutive 10-min averages of %PPFD on overcast days: r^2=0.83 and p<0.001.

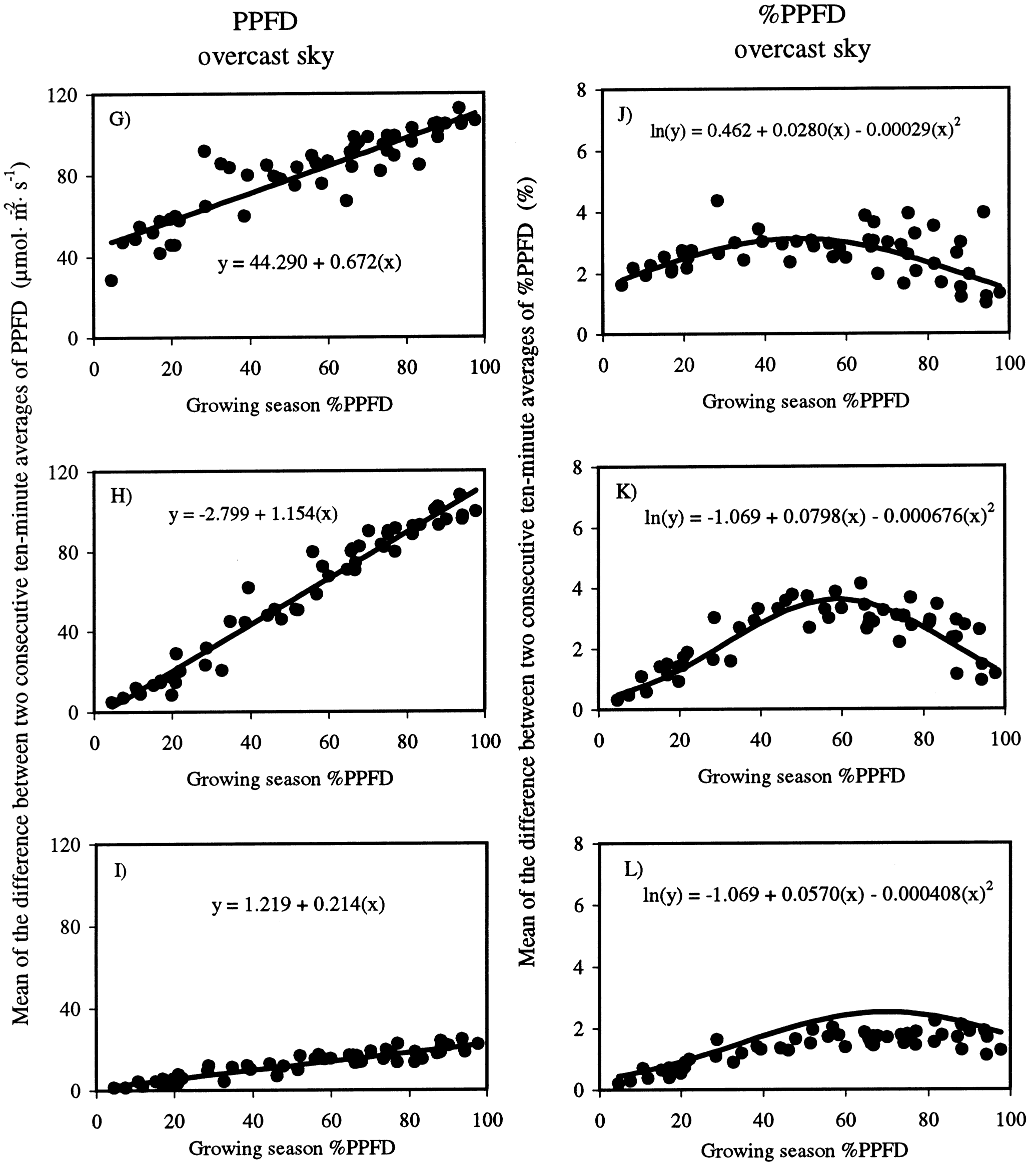


Fig. 1. (*Continued*).

above the forest floor up to the upper canopy where light availability was high. Similarly, microsites receiving high GSP exhibited lower CV_w than microsites with low GSP in the maple canopy stand. On overcast days, the slopes were only marginally significantly different from 0 ($p>0.04$) for the PPFD (Fig. 2G–I). CV_w for the %PPFD on overcast days were generally <20% (Fig. 2J–L). CV for the %PPFD as low as 1% has been reported beneath a *Quercus acutissima* forest and was attributed to the stability of diffuse light transmission under overcast sky conditions (Oshima et al., 1997).

Frequency of sunflecks greater than 250 µmol m^{-2} s^{-1} increased with increasing GSP (Fig. 3). Analysis of covariance showed that the intercept was significantly higher and the slope was significantly

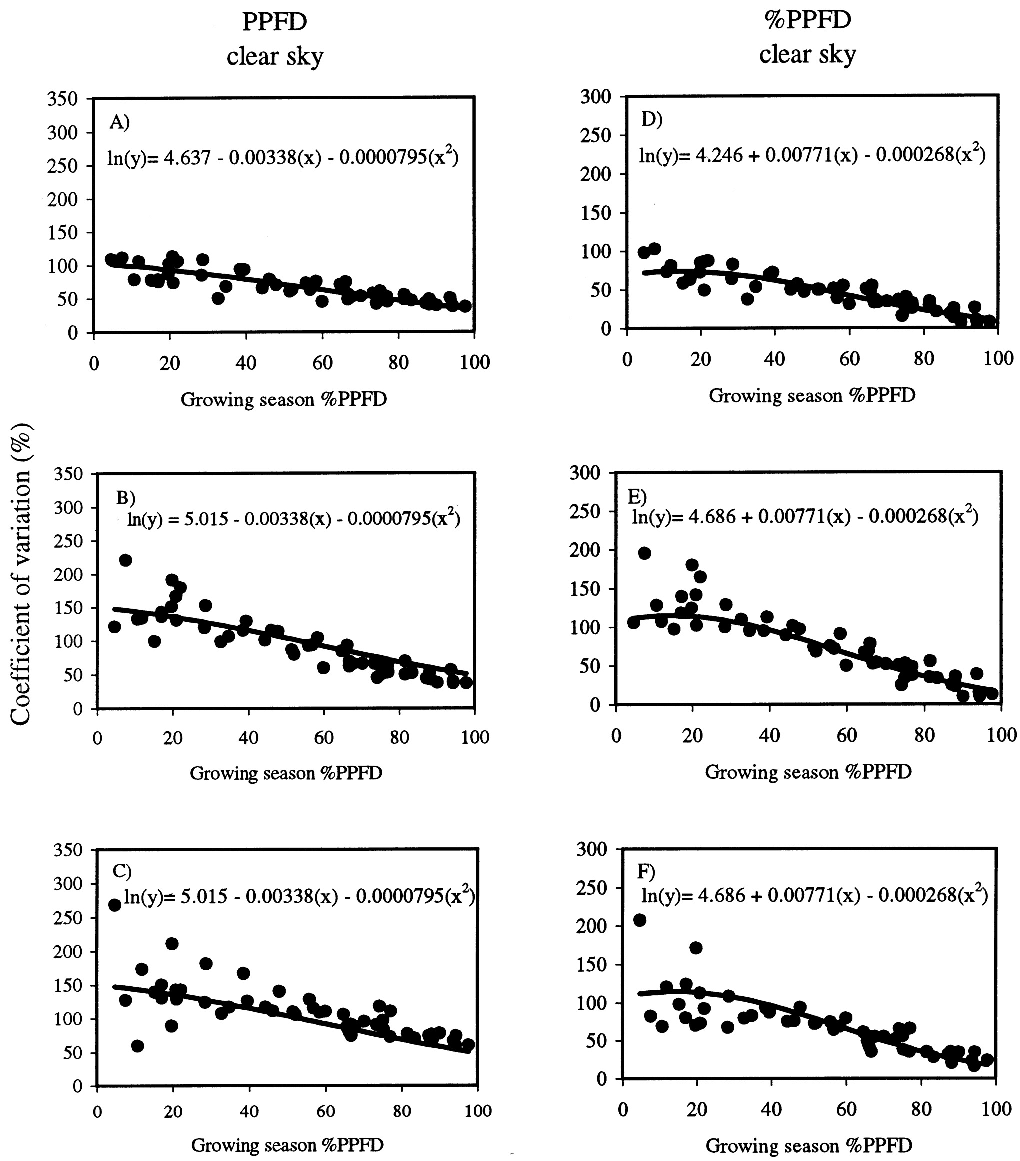


Fig. 2. Coefficient of variation (CV_w) of the 10-min averages of PPFD and %PPFD in May (A, D, G, J), July (B, E, H, K), and September (C, F, I, L) under clear and overcast sky conditions for understorey microsites ranging from 4.7 to 97.7% growing season PPFD. Relationships were calculated from covariance analysis. R^2 and probabilities of the models are as follows: CV_w of the 10-min averages of PPFD on clear days: $r^2=0.74$ and $p<0.001$, CV_w of the 10-min averages of %PPFD on clear days: $r^2=0.83$ and $p<0.001$, CV_w of the 10-min averages of PPFD on overcast days: $r^2=0.81$ and $p<0.001$, and CV_w of the 10-min averages of %PPFD on overcast days: $r^2=0.44$ and $p<0.001$.

lower ($p=0.0001$) in May compared to July indicating that sunfleck frequency was greater in May than in July. A decrease in sunfleck frequency from the beginning to the middle of the growing season has also been reported beneath a tall grass canopy (Tang et al., 1992). This could explain the decrease in the mean of the difference between two consecutive 10-min averages of PPFD and %PPFD from May to July for microsites receiving <20% GSP. Sunfleck frequency and light variability were higher in May than

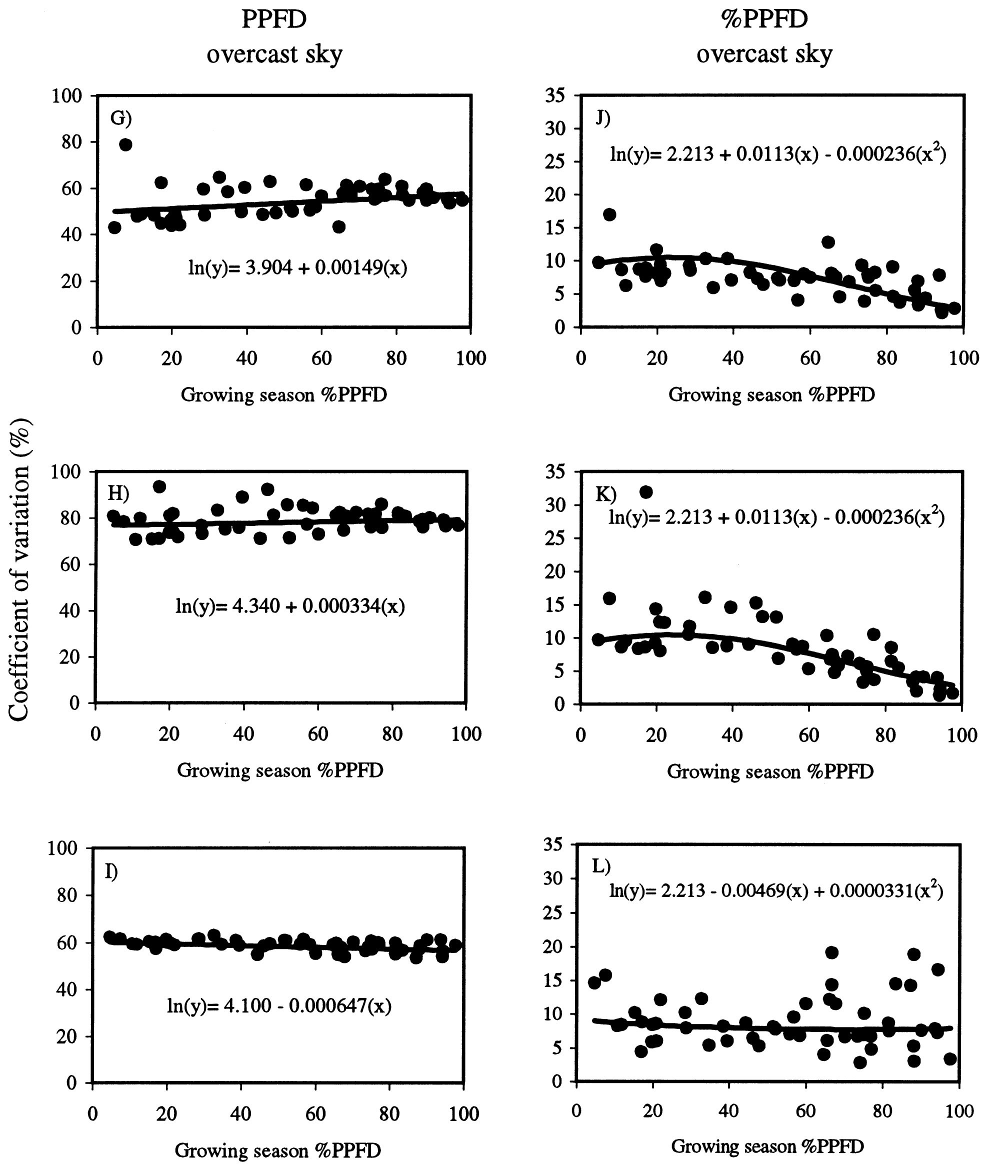


Fig. 2. (*Contineud*).

in July for these microsites. Baldocchi et al. (1986) reported that the presence of sunflecks in understorey microsites where most of the light consists of background diffuse light increases light variability. This was probably the case for these microsites in May where sunflecks probably reached the understorey in an irregular temporal pattern due to the presence of maple clumps and developing leaves. In July, lower sunfleck frequency coupled with lower mean daily PPFD and lower mean daily %PPFD (see seasonal light variability) may be responsible for the small differences between consecutive 10-min averages of PPFD and %PPFD. Similarly, the frequency distribution of %PPFD has been shown to be less variable when sunflecks were absent (Ross et al., 1986).

The relative contribution of sunflecks to daily PPFD also increased with increasing GSP with a sharp increase for microsites between 4 and 40% GSP

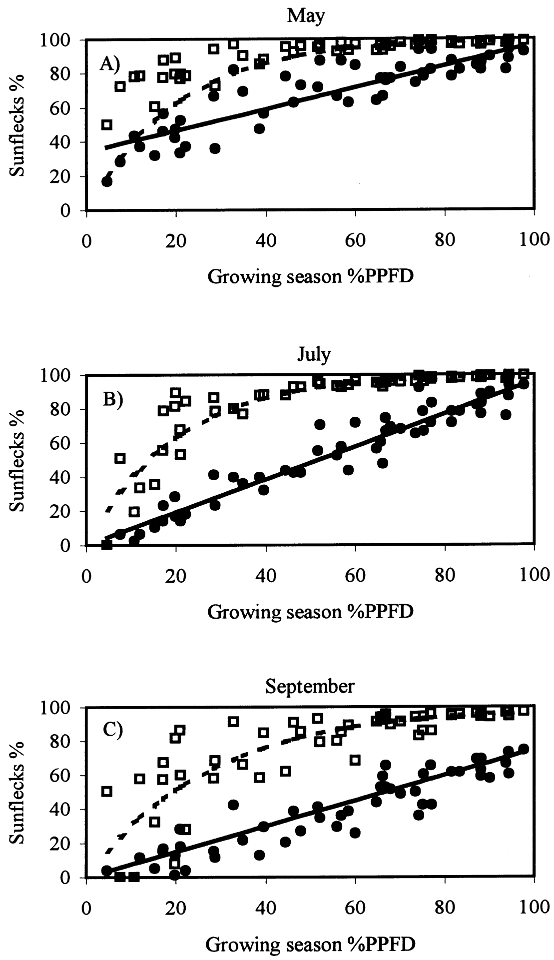


Fig. 3. Daily frequency and relative contribution to daily PPFD of sunflecks $>250\,\mu mol\,m^{-2}\,s^{-1}$. Frequency is illustrated as solid circles and solid lines in May ($y=33.954+0.629x$), July ($y=0.00443+0.962x$), and September ($y=0.00443+0.747x$). Relationships between daily frequency of sunflecks and GSP were calculated from covariance analysis ($r^2=0.90$ and $p<0.001$). Relative contribution to daily PPFD is illustrated as open squares and dotted lines in May ($y=100.1(1-\exp(-0.0487x))$, $r^2=0.95$, $p<0.001$), July ($y=100.1(1-\exp(0.0495x))$, $r^2=0.98$, $p<0.001$), and September ($y=100.1(1-\exp(-0.0356x))$, $r^2=0.95$, $p<0.001$).

(Fig. 3). The relative contribution of sunflecks for microsites receiving >60% GSP showed little variation throughout the growing season since it remained above 80%. Beneath aspen and white birch stands with a daily %PPFD of 9%, the relative contribution of sunflecks $>250\,\mu mol\,m^{-2}\,s^{-1}$ was 28 and 53%, respectively (Messier et al., 1998). This is in the range of 20 to 50% reported in the young maple canopy for microsites receiving about 9% GSP. Despite their low frequency, sunflecks make a substantial contribution to daily PPFD for microsites with low GSP. For example, sunflecks showed a frequency of <30% during the day, but a relative contribution of 20–80% of daily PPFD for microsites receiving <20% GSP. This disproportionate contribution of sunflecks to daily PPFD compared to their frequency has also been reported for other vegetation canopies (Chazdon and Fetcher, 1984; Tang et al., 1992; Baldocchi and Collineau, 1994). The large contribution of sunflecks to daily PPFD can be explained by the high photon flux density contained in a sunfleck, which can be 100 times that of the background of diffuse light environment (Baldocchi and Collineau, 1994).

3.2. Day-to-day light variability over the growing season

The mean difference between consecutive daily PPFD increased with increasing GSP (Fig. 4A). It ranged linearly ($r^2=0.95$, $p<0.001$) from 0.45 to $10.26\,mol\,m^{-2}$ per day for microsites receiving between 4.7 and 97.7% GSP. This trend is similar to the mean of the difference between consecutive 10-min averages in PPFD on overcast sky conditions reported for diurnal light variability. For microsites receiving low GSP, little PPFD reached the understorey, so differences between consecutive days in total PPFD were lower in absolute values.

CV_d of both daily PPFD and daily %PPFD were higher for low GSP microsites than microsites that received more light (Fig. 4B and D). CV_d of the daily sum of PPFD reached 102% for the 4.7% GSP microsites and then remained stable at about 50% for microsites between 20 and 100% GSP. This trend is consistent with the higher CV of mean daily PPFD reported in closed tropical rain forest microsites (CV=44.4%) compared to clearings (CV=14.9%) (Chazdon and Fetcher, 1984). CV_d reported for low GSP microsites in the young bigleaf maple canopy (CV_d up to 102%) are higher than the ones reported by Chazdon and Fetcher (1984), but this difference could be attributed to phenoseasons due to the drastic changes in bigleaf maple canopy cover at the beginning and the end of the growing season. CV_d of daily %PPFD decreased from 112 to 3% with increasing

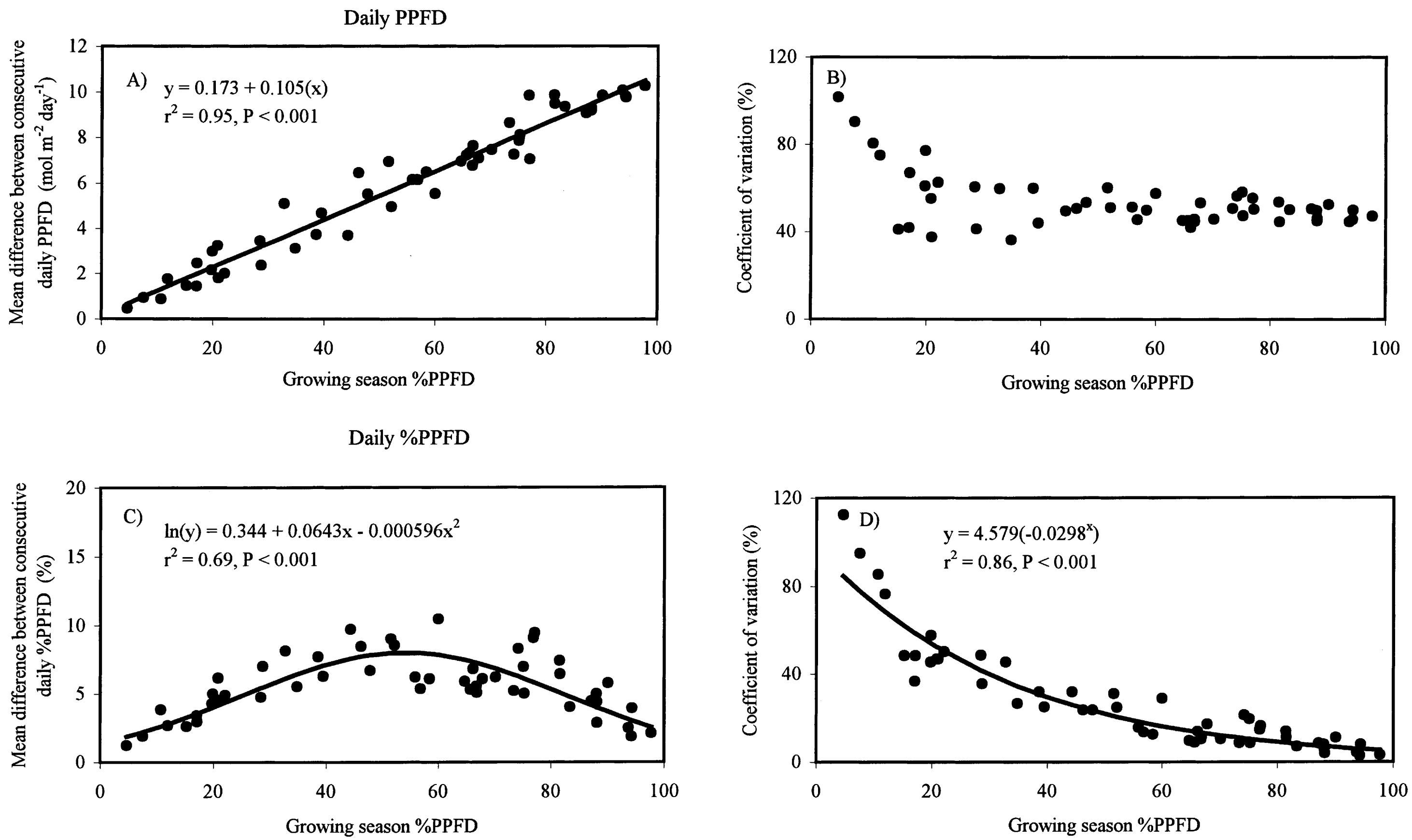


Fig. 4. Mean difference between consecutive daily PPFD (A) and %PPFD (C) and coefficient of variation of the daily PPFD (B) and %PPFD (D) for 52 understorey microsites ranging from 4.7 to 97.7% growing season PPFD. Days ranged from 18 May to 14 October 1996. No relationship was developed for the coefficient of variation of daily PPFD because linearity and homoscedasticity could not be achieved.

GSP. Daily percentage of irradiance varies much more from day to day in the understorey than in the open since the contribution of direct light to total irradiance is more variable in the understorey (Anderson, 1970).

The mean difference between consecutive daily %PPFD measurements was higher for microsites receiving between 20 and 80% GSP than for microsites with lower or higher levels of GSP (Fig. 4C). As mentioned previously, these microsites also exhibited high variability from one 10-min period to the next during July and September. Direct light penetration is influenced by the interplay between canopy gaps and position of the solar disk, as well as the above sky conditions (Rich et al., 1993). Consequently, the presence (or absence) of clouds when the sun is aligned with canopy openings on partly sunny days may decrease (or increase) mean daily %PPFD for these microsites and result in large differences between consecutive days.

3.3. Seasonal light variability

Seasonal light variability was characterised as the ratio between May and July and between July and September measurements of mean daily PPFD and mean daily %PPFD for both clear and overcast sky conditions. Microsites with <50% GSP received up to eight times more light in May than in July on both clear and overcast sky conditions (Fig. 5). One of the major change in deciduous forest is the development of the canopy at the beginning of the growing season. A decrease in light at the beginning of the growing season was also reported from other studies in deciduous forests (Anderson, 1964; Hutchison and Matt, 1977; Baldocchi et al., 1984; Ross et al., 1986; Constabel and Lieffers, 1996) and tall grass (Tang et al., 1992). In the young maple canopy, microsites with <40% GSP showed the largest decrease from May to July compared to microsites with more GSP. Similarly, Anderson (1964) reported that the larger the difference in canopy cover between the beginning and the middle of the growing season, the larger the decrease in the absolute amount of light availability in the middle of the growing season.

From July to September, most microsites received more mean daily PPFD and %PPFD in July than September on clear days. This is explained by the fact that the mean daily PPFD was higher in July than in September on both sunny days (Table 1). However, some microsites with <40% GSP actually had higher mean daily PPFD and mean daily %PPFD in September since their ratios were <1. Light availability has been observed to remain stable or to decline slowly in deciduous canopies from the middle of the summer to the beginning of the fall. For example, mean daily %PPFD remained stable from June to September in a *Quercus–Carya* forest (Baldocchi et al., 1984). Similarly, daily total PPFD was relatively constant from July to September in a grass canopy (Tang et al., 1992). In contrast, Hutchison and Matt (1977) report that mean daily radiation declined during the summer in a deciduous canopy. They suggest that this was because the degree of canopy openings along the solar path decreases as the solar path declines after the summer solstice. Because of the lower solar elevation above the horizon in September (45° compared to 62° in July in the present study), the path length is increased and more light is attenuated by vegetation elements (Holmes, 1981). The relationship between the location of canopy gaps and the solar path has a strong influence on light penetration in forests. Even though the proportion of gaps in the canopy is higher at the zenith (Anderson, 1966; Hutchison et al., 1980), this region constitutes only a small portion of the hemisphere (Hutchison et al., 1980) and most light penetration to the understorey comes from angles between 50° and 70° above the horizon in a range of temperate forests (Canham et al., 1990; Canham et al., 1994; Easter and Spies, 1994). Consequently, the lower solar elevation in September may have increased the fraction of direct light under the young bigleaf maple canopy for some microsites with canopy gaps not centred around the zenith, but located lower above the horizon. The use of many types of microsites could be responsible for the broad range of light variability reported in the young bigleaf maple canopy. This range in light variability may be reduced when plot averages are used instead of values from individual microsites.

Microsites with as low as 50% GSP received as much mean daily PPFD and mean daily %PPFD in July as in May on clear and overcast days despite changes in canopy leaf area index. Direct light passing through the canopy either reached the forest floor unobstructed with full intensity or with less intensity because of scattering by maple stems and penum-

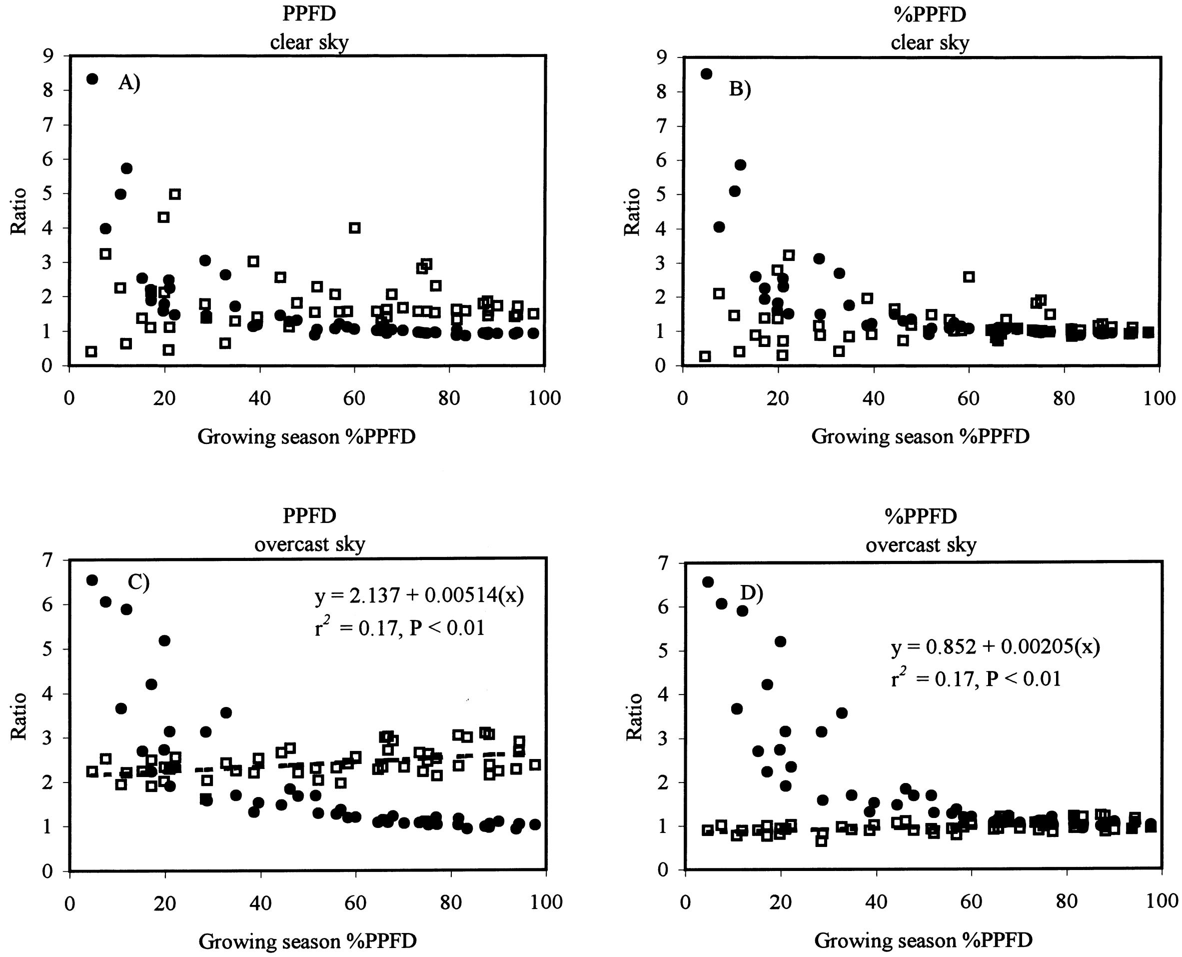


Fig. 5. Ratio of mean daily PPFD (A, C) and %PPFD (B, D) from May to July (●) and from July to September (□). Data are illustrated on clear (A, B) and overcast (C, D) sky conditions. The linear regressions are illustrated for the ratio of mean daily PPFD and mean daily %PPFD from July to September on overcast days. No relationship is shown when linearity and homoscedasticity could not be achieved. When the ratio equals 1, mean daily PPFD or %PPFD is constant from May to July or from July to September. When the ratio is >1, mean daily PPFD or %PPFD is higher in May than in July or in July than in September. When the ratio is <1, mean daily PPFD or %PPFD is lower in May than in July or in July than in September.

bra effect (Reifsnyder et al., 1971). Our hypothesis is that even though leaves were just starting to develop during May, sunlight was still reduced by the stems of maple clumps. In this young bigleaf maple stand, maple clumps originated from sprouts and there were about 22 stems per clump with a sum of stem area of about 6185 cm^2 per clump. Also, the sun subtends an angular diameter of 0.5° (Stenberg et al., 1995), so spaces of <0.5° between stems could have resulted in penumbral light on clear days. Another explanation is that canopy development effectively reduced the frequency of sunflecks >250 $\mu mol\,m^{-2}\,s^{-1}$ in July compared to May, but their contribution to daily PPFD was still above 80%. This may explain why mean daily PPFD and mean daily %PPFD were comparable in May and July for microsites as low as 50% GSP.

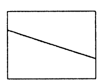
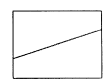
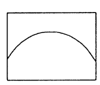
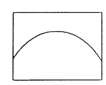
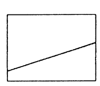
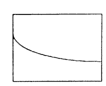
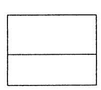
Mean daily PPFD was about 2.5 times higher in July than in September for all microsites on overcast sky conditions. This decrease is comparable to the decline in above-canopy light for these two periods (420 μmol m^{-2} s^{-1} in July compared to 167 μmol m^{-2} s^{-1} in September, see Table 1). The decrease in mean daily PPFD from July to September is related to the decline in solar elevation and not to changes in GSP.

All microsites received as much mean daily %PPFD in July as in September on overcast days since the ratio remained close to unity. This pattern was also reported by Hughes et al. (1985) on overcast days in a *Quercus robur* forest. Percent light has been shown to be very stable throughout the day in the understorey on overcast days (Messier and Puttonen, 1995) and could be used as an index of daily light availability (Washitani and Tang, 1991; Parent and Messier, 1996; Gendron et al., 1998). Provided that canopy leaf area does not change, the present study demonstrates that mean daily %PPFD on overcast days remained the same from the middle to the end of the growing season and is not influenced by the decline in solar elevation over this period.

4. Potential implications of light variability on plant growth

It is generally believed that open, high light microsites are temporally more variable than low light microsites (Bazzaz, 1979; Bazzaz and Carlson, 1982). Such an affirmation needs to be revisited since this study shows that light variability may or may not be higher in high light microsites depending on: (1) whether absolute or percent PPFD values are measured; (2) the level and type of variability measured; (3) the period during the growing season; and (4) the sky conditions. The various trends in light variability are summarised in Table 2. The relationship between microsite and light variability is influenced by the method of measurement used to characterise light variability. For a particular microsite, light can differ depending on whether it is measured at the diurnal or the day-to-day level. Use of either the mean difference between consecutive readings or the CV can also lead to

Table 2
General trend of diurnal and day-to-day PPFD and %PPFD variabilities, as measured using the mean of the differences between two consecutive 10-min averages or days and the coefficient of variation (CV) for 52 understorey microsites ranging from 4.7 to 97% growing season PPFD

Types of light variability[a]			
Diurnal[b]		Day-to-day[c]	
Mean of the difference between two consecutive 10-min averages of PPFD and %PPFD on clear days in May CV of PPFD and %PPFD on clear days in May, July, and September CV of %PPFD on overcast days in May, July, and September		Mean difference between consecutive daily PPFD	
Mean of the difference between two consecutive 10-min averages of PPFD and %PPFD on clear days in July and September Mean of the difference between two consecutive 10-min averages of %PPFD on overcast days in May, July and September		Mean difference between consecutive daily %PPFD	
Mean of the difference between two consecutive 10-min averages of PPFD on overcast days in May, July, and September		CV on the total daily PPFD and %PPFD	
CV of PPFD on overcast days in May, July, and September			

[a] The *Y*-axis is the relative measure of light variabilty and the *X*-axis is the growing season %PPFD ranging from 0 to 100%.
[b] Diurnal light variability was calculated on representative clear and overcast days in May, July, and September.
[c] Day-to-day light variability was calculated from 18 May to 14 October.

different conclusions. Since different levels and types of light variability may have different effects on plants, emphasis should be placed on the influence of different levels and types of light variability on plant growth.

On a diurnal basis, the type of light variability measured by the mean of the difference between two consecutive 10-min averages of PPFD and %PPFD may relate more closely to changes in plant traits such as instantaneous photosynthesis, stomatal responses, conductance, and photosynthetic induction (sensu Ackerly, 1997) than the CV_w, which measures the overall light variability during the day. For example, *Carya ovata* seedlings grown under similar daily PPFD exhibited larger stem biomass, basal diameter, and secondary root dry weight in experimental short duration sun patch environments than long-duration sun patch environments (Robison and McCarthy, 1999). Species differences in shade tolerance, light compensation points, and other features should also be considered in the selection of a suitable measure of light variability. For example, shade-intolerant species are less efficient at capturing elusive sunflecks than shade-tolerant species (Paliwal et al., 1994). A microsite characterized by frequent sunfleck events is likely to have a higher value of the mean of the difference between two consecutive 10-min averages of PPFD and %PPFD.

The type of light variability measured by the CV_w of the 10-min averages of PPFD and %PPFD indicates the relative light variability within a day. It is most likely to influence photosynthetic capacity, photoperiodic responses, and canopy display (Ackerly, 1997). Wayne and Bazzaz (1993) demonstrated that seedlings of *Betula populifolia* and *B. alleghaniensis* grown under similar total daily PPFD, but different coefficients of variation showed significant differences in leaf-level physiology, biomass allocation, and phenotypic plasticity.

Plant traits, such as photosynthetic acclimation, leaf morphology, and plant growth, can track day-to-day light variability (Ackerly, 1997). For example, in simulations using the tropical pioneer tree species *Heliocarpus appendiculatus*, leaf display was the morphological trait best able to respond to daily variability in the light environment (Ackerly, 1997). The mean difference between consecutive daily PPFD or daily %PPFD and the CV_d may provide useful evaluation of this type of variability and may correlate well with these types of plant responses. However, further research is needed to examine how these different types of light variability will influence plant growth.

The effects of various microsites on light variability change according to the period during the growing season over which it is being measured. On clear days, the mean of the difference between two consecutive 10-min averages of PPFD was larger for microsites with $<$20% GSP in May, but larger for microsites with 20 to 80% GSP in July and September. Sky conditions are also important to consider since the mean of the differences between two consecutive 10-min averages of PPFD and %PPFD as well as the CV_w of PPFD and %PPFD were generally lower under overcast than clear sky conditions. Thus, ecosystems in Continental or Tropical-humid climates with mostly overcast sky conditions could exhibit different light variabilities for a similar microsite from Mediterranean climates with mostly clear sky conditions. Light variability may reflect on plant performance, since, for a similar daily PPFD, plant growth is favoured in uniform light environments compared to variable light environments (Sims and Pearcy, 1993; Wayne and Bazzaz, 1993).

5. Conclusion

Different levels and types of light variability were characterised in the young bigleaf maple stand. In this stand, light variability was affected by canopy development, solar elevation, and sky conditions and the influence of each of these factors was often related to the growing season %PPFD of microsites. However, these results indicate that it is not possible to generalise which microsites are more variable than others, since microsites are subjected to various levels and types of light variability. Instead, light variability should be evaluated according to how it affects plant growth. Studies assessing the effect of light variability on plant growth have generally examined only one selected type of light variability. Future studies should include examination of different levels and types of light variability to better describe effects of light microclimates on plant responses.

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