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Characteristics of small-scale heterogeneity in light availability within a *Miscanthus sinensis* canopy

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To examine the small-scale variations in light and space availability, photon flux density (PFD) at 20 cm aboveground was measured at 2 cm intervals along each of four 160 cm horizontal transects under an overcast sky condition in a *Miscanthus sinensis* Anderss grass canopy. Two characteristics were identified for the variation patterns of PFD penetration along transects; the predominant variations of PFD penetration prevailed at the scales usually larger than 10 cm, and the point-to-point fluctuations occurred everywhere. Spatial autocorrelation coefficients of PFD penetration along transects were highly positive (>0.5) over the lag distances from 2 to 6 cm, while those of the point-to-point fluctuations exhibited a random series. Spectrum analysis showed a higher spectrum density at the lower frequency, that is, at the higher periodicity, which indicated that the variation of PFD penetration was mainly due to the patchy distribution of grass canopy. PFD-available spans along the transects and contour maps were examined to evaluate the microsites fulfilling both PFD and space requirements in the growth of *Quercus serrata* Thunb. seedlings. More than 75% of the spans with PFD penetration constantly exceeding 0.04 were shorter than 8 cm, which suggests that a large proportion of high PFD spots may not be used by *Q. serrata* seedlings in the grass canopy because of the limitation of availability in space. The spatial heterogeneity of PFD at small scales may be of great importance in the succession of *M. sinensis* grass communities.

Key words: grasslands; light environment; microsite; photon flux density; spatial heterogeneity.

INTRODUCTION

Most theoretical works on the light penetration in plant canopies are based on the assumption that the plant canopy is horizontally homogeneous and extensive, plane parallel, and optically isotropic turbid medium filled densely with small scattering elements (e.g. De Wit 1965; Miller & Norman 1971). However, plant canopies are not always homogenous, such as *Miscanthus sinensis* Anderss. canopies that are highly heterogeneous with patches of various sizes (Iwaki *et al.* 1985). The heterogeneity of canopy structure would affect the spatial variation of light within plant canopies.

Recently, spatial heterogeneity of light environments at small scales from centimeters to meters within plant canopies is receiving increasing attention (Silvertown *et al.* 1988; Tang *et al.* 1990; Williams 1992). Silvertown *et al.* (1988) showed a marked heterogeneity in R/FR ratios in a 160 cm^2 plot under a grass canopy and discussed its ecological implications. Within *M. sinensis* grass canopies, the spatial distribution of photon flux density (PFD) is highly heterogeneous (Tang *et al.* 1989). The light availability at the scale of individual seedlings affects remarkably the characteristics of photosynthetic induction response, biomass allocation and morphological plasticity in *Quercus serrata* Thunb. seedlings within the grass canopies (Tang *et al.* 1990; Tang *et al.* 1992a; Tang *et al.* 1993). These studies suggest that the small-scale heterogeneity of PFD seems to play an important role in the establishment of tree seedlings within grasslands. Therefore, characteristics of PFD heterogeneity at small scales, especially at the scale of individual tree seedlings, must be understood in order to reveal further their possible ecological implications in the

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replacement process from grasslands to tree communities.

Since the pioneer work on the light penetration by Monsi and Saeki (1953), many studies have focused on the intensity of light within plant communities. A threshold value of light intensity has usually been set for the evaluation of a particular biological process. An average of 0.04 in light penetration, for example, has been considered as a critical value for the establishment of tree seedlings within grass canopies (Monsi & Oshima 1955). However, even if the light availability in a microsite is high enough, the microsite can not be utilized if its physical space is too small for a particular plant or for a specific biological process. Therefore, it would be insufficient or even misleading unless both the light and space availabilities are considered.

In the present study, our objective was to characterize the spatial variation of PFD at the centimeter scale on a horizontal plane and evaluate the availability of microsite from both light and spatial requirements within the grass canopy.

MATERIALS AND METHODS

Study site

Light measurements were made in the *M. sinensis* grassland on the southern campus of the University of Tsukuba, Tsukuba, Japan. The grassland has been developed since 1976 from an abandoned field. The main associated species in the study site were *Amphicarpaea edgeworthii* Benth. var. *japonica* Oliver, *Artemisia princeps* Pampan., *Erigeron annuus* Pers., *Glycine soja* Sieb. et Zucc., *Imperata cylindrica* P. Beauv. var. *koenigii* (Retz.) Durand et Schinz and *Phragmites australis* Trin. The aboveground biomass of the stand in late September, 1989, was 950 g m^{-2} with a leaf area index (LAI) of 3.85 and a mean canopy height of about 190 cm.

Light Measurement

PFD within the grass canopy was measured with Koito quantum sensors (KOITO, IKS-25) from 6 : 30 to 8 : 00 local time on 22 July 1989. The active area of the sensor is 0.785 cm^2. The 90% response time of the sensor is 500 μs and the measuring range is 0–3000 μmol photon m^{-2} s^{-1}. Before the measurement, the Koito quantum sensors were calibrated under sunlight and artificial shade against a LI-COR Model 190s Quantum Sensor. Up to 16 sensors were mounted at 2 cm intervals on a 1 m-long aluminium bar. The PFD from each sensor was recorded at 1 s interval by a data logger (Eto Denki Thermdac E), which was controlled by a personal computer (PC-9801 INS/T, NEC, Japan).

Measurement of PFD was performed within a plot of 2×2 m^2 in the *M. sinensis* grassland (Fig. 1). PFD at 20 cm aboveground was recorded at 2 cm intervals along each of four transects. The measuring height is approximate to the initial height of the current year seedlings of *Q. serrata*. The transects were located parallelly at a neighbor distance of 40 cm. The other details were described elsewhere (Tang *et al.* 1989). After the measurement of PFD, the grass was cut and the patch size of *M. sinensis* grass was measured in length and width to illustrate the horizontal distribution of grass patches (Fig. 1).

Various factors including solar elevation, sky conditions and canopy structure cause the spatial heterogeneity of light distribution within canopies. Measurements were taken under an overcast sky and windless weather conditions, when the interferences from direct solar radiation and leaf vibration caused by wind were not factors. The readings were recorded on a 3.5 inch floppy disk. The data were transferred to a Macintosh computer IIsi for analy-

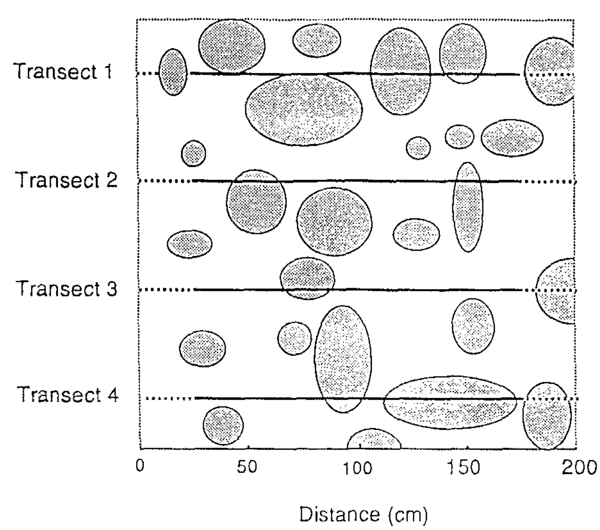

Fig. 1. Distribution of *Miscanthus sinensis* patches. Each patch was measured in two orientations (North–South and East–West) and then mapped as ellipses.

sis. All analysis was performed with PFD penetration, the ratio of PFD within canopy to PFD above canopy. In this study, PFD penetration shared the same definition as the diffuse site factor used in our previous studies. Diffuse site factor has been proved to be a good indicator for microsite light availability (Tang *et al.* 1992b).

Spatial autocorrelation

In general, spatial autocorrelation analysis is similar to the autocorrelation analysis of time series, except that in the latter case only one direction is considered. Let X_s be a spatial series of the PFD ($s = 1, \ldots N$). A spatial autocorrelation coefficient (r_k) is a measure of the dependence of the value at one point on the values at neighboring points, which is given by:

$$r_k = \sum_{s=1}^{N-k} (X_s - M)(X_{s-k} - M) / \sum_{s=1}^{N} (X_s - M)^2, \quad k = 0, 1, \ldots N-1 \qquad (1)$$

where r_k is called the spatial autocorrelation coefficient at lag k for the spatial series X_s with the mean M.

To reveal the point-to-point variations of PFD penetration, we differentiated the original PFD penetration $PFD(s)$ and obtained an absolute data set $PFDd(s)$:

$$PFDd(s) = abs(PFD(s+1) - PFD(s)) \quad s = 1, 2, 3, \ldots N-1 \qquad (2)$$

where $abs\ (x)$ takes the absolute value of x.

Spectrum analysis

To discover the hidden periodicity in the PFD data along a given transect, we examined the estimation of the spectral density function $I(V_r)$, which is the Fourier transform of the sample autocorrelation coefficients and is calculated as:

$$I(v_r) = [(\sum_{s=1}^{N} x_s \cos 2\pi rs/N)^2 + (\sum_{s=1}^{N} x_s \sin 2\pi rs/N)^2]/N\pi \qquad (3)$$

where $v_p = 2\pi r/N$ is the frequency at period of r for a spatial series (x_s) with a total observations of N. The plot of $I(v)$ against v can be called the periodgram. A characteristic of equation (3) is that the total area under the periodgram is equal to the total variance of the spatial series (Chatfield 1989). Therefore, the relative areas under different frequency correspond to the relative contribution of variance.

To obtain a reliable estimate of the spectrum, it is often recommended that between 100 to 200 observations is the minimum. However, reliable estimates may be obtained even with the number of observations (N) less than 100, if the data are prewhitened or only large peaks are used for discussion (Chatfield 1989). Since the observations are less than 100 (N = 80) in the present study, we only focused on the very large peaks, which may be related to the patch structure of grass canopy.

Computer programs for calculating the autocorrelation coefficients and spectrum were written in Quick Basic for Macintosh computer. The programs were checked with a test data set (Wei 1990).

High PFD span and contour map

To examine the spatial characteristics of PFD-available microsites, the spans with PFD penetration constantly higher than a threshold value were picked up from the transect data. Two threshold values of PFD penetration were used in the study. The lower threshold value of 0.02 was an approximate PFD penetration required for a positive CO_2 fixation in shade leaves of *Q. serrata* seedlings (Tang *et al.* unpubl. data). The higher value (0.04) was in sun leaves and also a critical value for the establishment of most heliophilic trees (Tang *et al.* unpubl. data; Monsi & Oshima 1955).

To have a two-dimensional image about the PFD-available microsite, a contour map was drawn with the application soft WingZ for Macintosh computer.

RESULTS

Horizontal distribution pattern of PFD penetration

As shown in Fig. 2, PFD penetrations along all the four transects were highly variable. Two general characteristics are recognizable for the variation

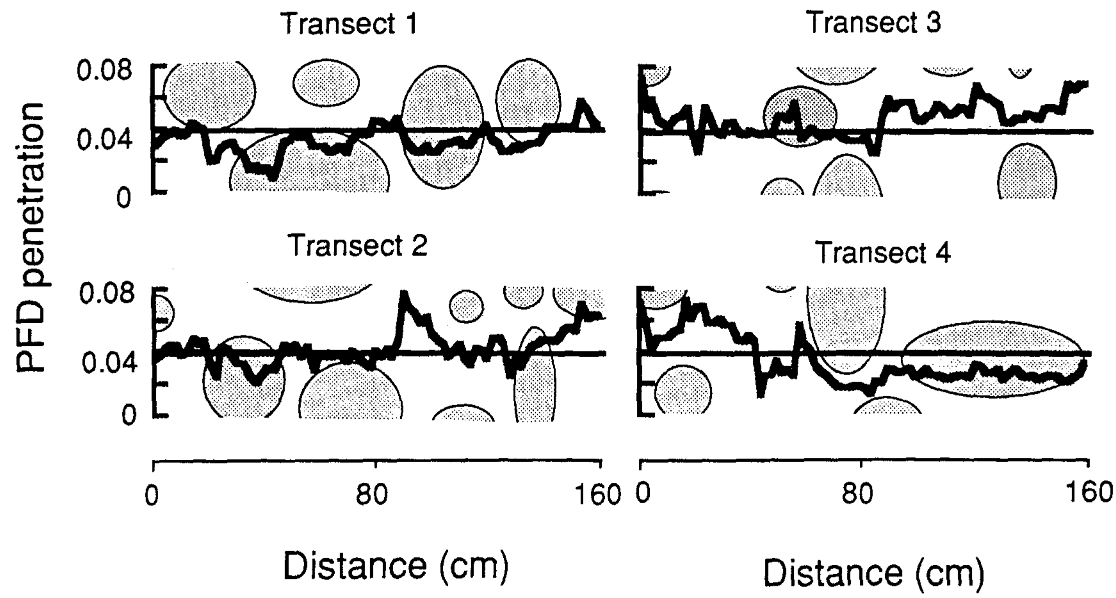

Fig. 2. Penetration of PFD on horizontal transects at 20 cm aboveground within a *M. sinensis* canopy. Measurement of PFD was carried out at 2 cm intervals along each transect. The transects spaced parallelly from 40 cm each other. The grass patch distribution along the transects is also shown by shaded ellipsoids.

patterns of PFD penetrations along each transect. First, predominant variations, that is, the long-phase variations of PFD penetration, prevailed at the scales usually larger than 10 cm. Second, the point-to-point fluctuation of PFD penetration, that is, the variation of PFD penetration between 2 cm, occurred everywhere. PFD penetrations were lower under the canopy of *M. sinensis* grass and higher in small gaps.

Spatial autocorrelation and spectrum properties of PFD penetration along transects

To analyze the relationship of PFD penetration between two points apart from various distances along a transect, spatial autocorrelation coefficients (SAC) were shown in Fig. 3. SAC were highly positive (>0.5) over the lag distances from 2 to 6 cm and then decreased rapidly with the increase of lag distance in general, but the SAC of transect 4 showed a slow decrease with the increase of lag distance (Fig. 3). Each transect showed a weak periodicity. Transects 3 and 4 exhibited positive SAC from 2 to 40 cm, while the other two transects showed negative SAC from 10 cm.

Spectral analysis was therefore carried out to determine the characteristics of hidden periodicity of PFD penetration along a transect. All the four transects showed a similar spectrum pattern: there was the highest spectrum density at the lowest frequency, that is, at the largest spatial period (Fig. 4).

Differential PFD penetration (PFDd) derived by equation (2) was examined to characterize the point-to-point fluctuations of PFD. Figure 5 shows the pattern of the relative frequency of PFDd (difference of PFD penetration variation between 2 cm). The percentage of PFDd decreased markedly with the increase in the variation values of PFD penetration between 2 cm points. About 20% of PFDd values were out of ± 0.01.

Characteristics of the point-to-point variations of the PFDd were examined by spatial autocorrelation analysis and spectrum analysis. PFDd was a significant random spatial series (Fig. 6) since almost all the SAC were within $\pm 2/\sqrt{N}$ except $k = 1$. The spectrum for the transformed data PFDd(s) showed no significant periodicity and indicated a random spatial series (data not shown).

PFD-available microsite

The frequency distributions of the spans with PFD constantly exceeding a threshold value are shown in

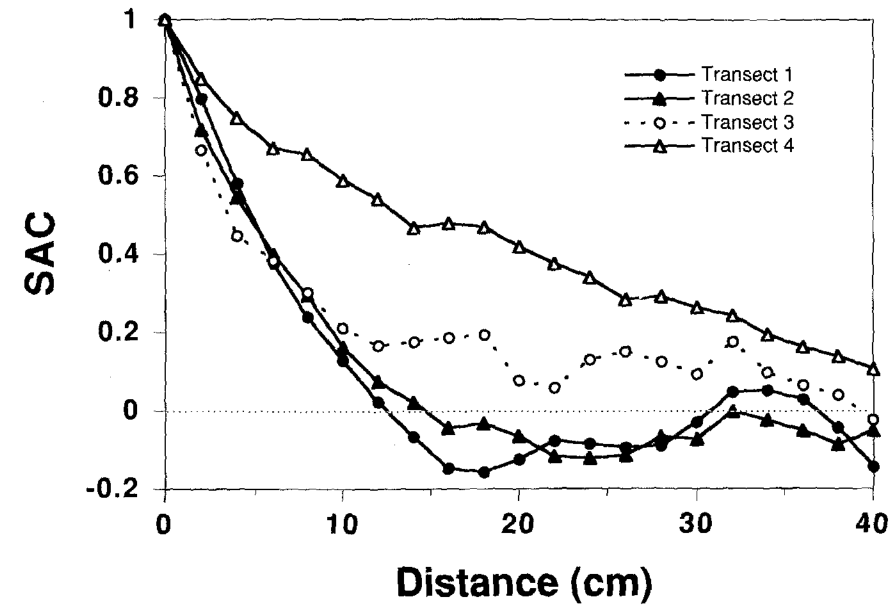

Fig. 3. Spatial autocorrelation coefficients for PFD penetration along the four transects.

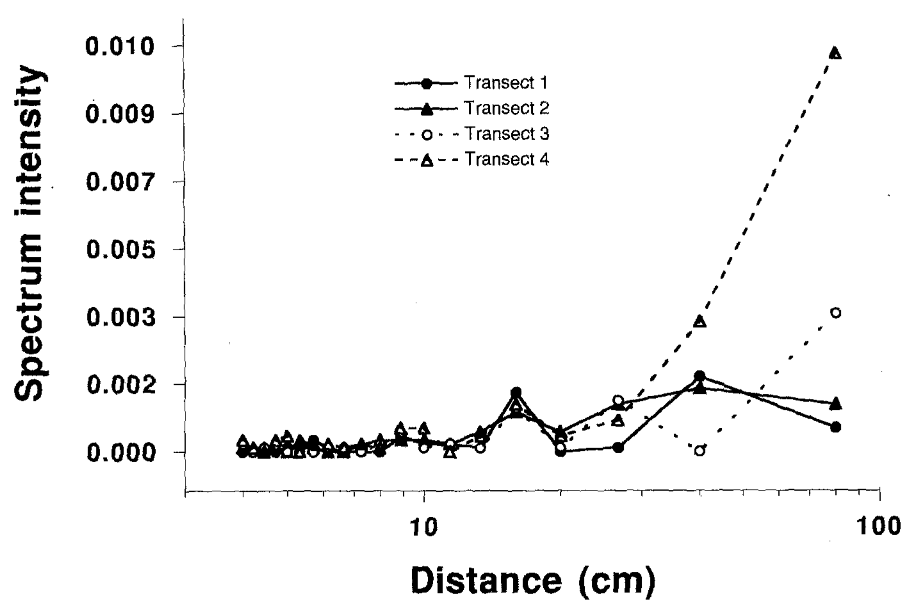

Fig. 4. Spectral density for PFD penetrations along the four transects.

Fig. 7. The distance of more than 90% high-PFD spans was longer than 8 cm for the lower threshold value of 0.02, but it was only about 25% for the higher threshold value of 0.04.

From the transect data in Fig. 2, we mapped the horizontal distribution of PFD penetration by contours (Fig. 8). There were marked variations in the size and number of microsites with PFD penetration above various threshold values. The contour map shows about 50% of total area (160 × 160 cm^2) with PFD penetration above 0.04.

DISCUSSION

Characteristics of PFD penetration along transects

The predominant variations in this study site may be caused by the patchy distribution of *M. sinensis* patches, while the point-to-point variations seem to be mainly due to the distribution of individual leaves and shoots of the grass.

Our previous study showed that PFD penetration

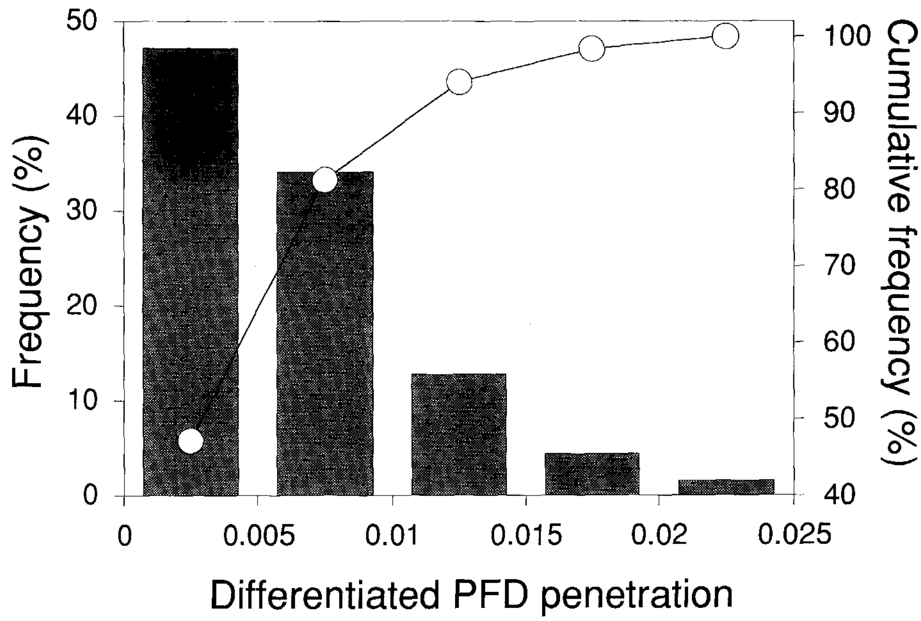

Fig. 5. Relative frequency of differentiated PFD penetrations between a 2 cm interval along four transects. Differentials of PFD penetrations are absolute values of PFD(s + 1) − PFD(s). (■), Frequency; (–O–), cumulative frequency.

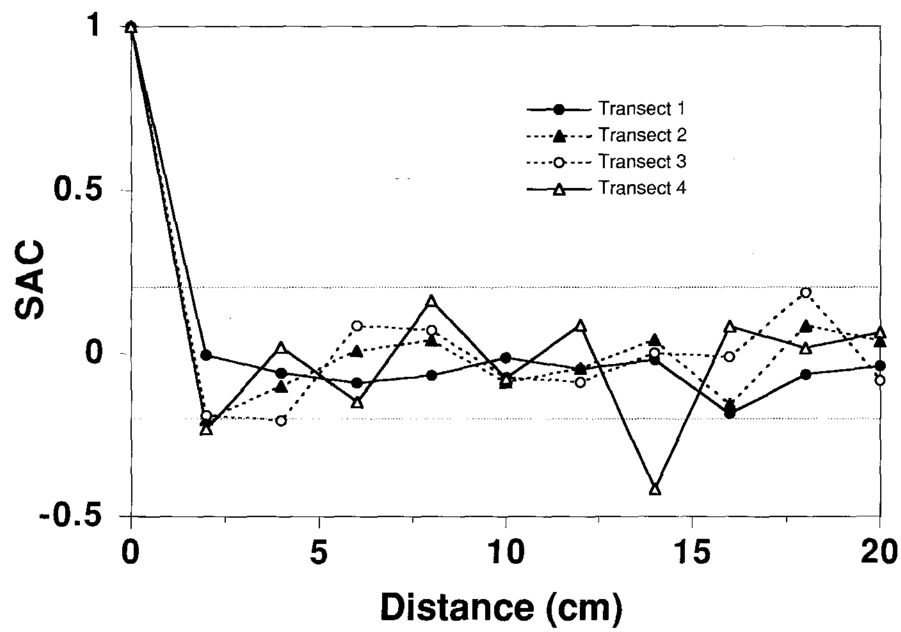

Fig. 6. Spatial autocorrelation coefficients for differentiated PFD penetrations along the four transects. Dotted lines indicate the significant range $\pm 2/\sqrt{N}$, where N is the number of lags.

along a transect within a *M. sinensis* canopy is a spatial short-term correlation series under an overcast sky condition (Tang *et al.* 1989). This spatial pattern was confirmed in the present study. However, the distance for the recovery of spatial autocorrelation coefficients was generally short (about 35 cm) in this study as compared with that obtained for the *M. sinensis* canopy in Honjo (Tang *et al.* 1989). Occurrence of small patches at a high density as observed in the present study might cause partly the rapid decrease of SAC with the increase of distance. Transect 4 showed a much slower decrease of SAC because of the large patches (Fig. 2).

A short-term correlation series has two characteristics: (i) an observation above the mean tends to be followed by one or more observations above the mean, and this is also true for the observations below the mean; (ii) autocorrelation coefficients for longer lag distances tend to be zero (Chatfield 1989). The high autocorrelation coefficients (SAC >0.5) for

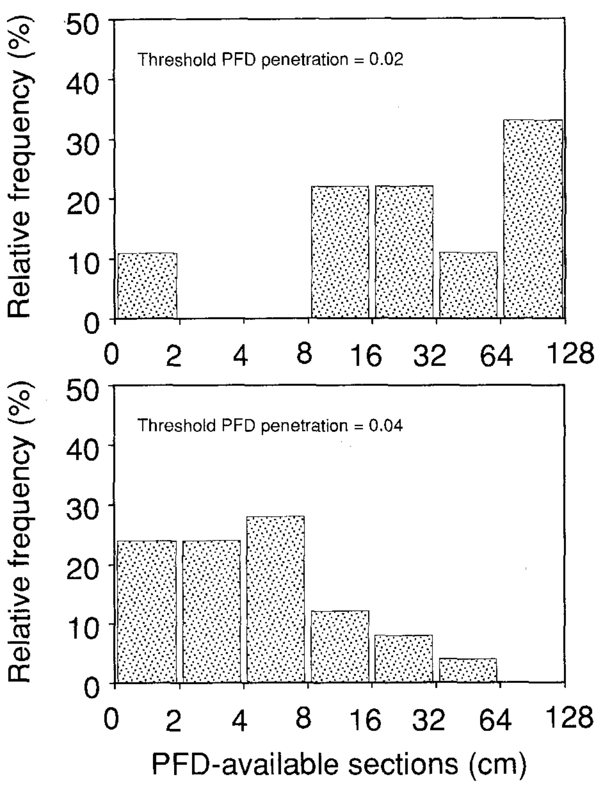

Fig. 7. Frequency distributions of the distance of spans with PFD penetrations constantly exceeding the threshold value of 0.02 (top) and 0.04 (bottom), respectively.

the lag distances from 2 to 6 cm as shown in Fig. 3 suggest that the spatial variation of PFD penetration is relatively small over a very short distance along a transect within the grass canopy. Peter and Smith (1990) proposed that the lag distance for positive SAC would approximate the diameter of patch size and estimated the canopy patch size ranging from 2.5 to 12.5–22.5 m in a mature forest on Barro Colorado Island. Positive autocorrelations differed among transects in this study. The positive autocorrelations from 2 to some 40 cm in three of the four transects suggest that the dimension of the patch structure in the *M. sinensis* canopy is much smaller than that in the forest.

Ripley (1978, 1981) compared several statistical approaches to the problems of spatial pattern analysis and concluded that spectral analysis performs reliably and gives a good indication of the type of departure from a random pattern. PFD penetration along a transect could not be characterized as a random series because of the distinct spikes in the grass canopy (Fig. 3). That all of the transects showed two spikes indicates a significant periodicity hidden in the transect data of PFD penetration, which may be due to the patchy structure of the grass canopy. The spectral density can be interpreted roughly as the relative variance at different frquency (Chatfield 1989). The large spikes at low frequency therefore took more than 90% of variance in PFD penetration along a transect (Fig. 6). This suggests that most variance in PFD penetration can be included within a distance of about 40 cm along a transect in the *M. sinensis* canopy.

Ecological implications of PFD variations at small scale

A threshold value of PFD penetration of 0.04 can be used for the evaluation of microsites for the establishment of most heliophilic trees (Monsi & Oshima 1955). The present study showed that there were four microsites above this threshold value in the 160 × 160 cm^2 *M. sinensis* grassland. These microsites each took a horizontal area ranging from 200 to 7650 cm^2. The horizontal area for an individual canopy of *Q. serrata* seedlings is almost always less than 400 cm^2 (Tang *et al.* unpubl. data). This suggests that part of these microsites could provide enough space for a 1 year seedlings of the tree. The number of the microsites available for heliophilic trees would increase if the canopy size of individual plants becomes smaller, and *vice versa*. On the other hand, the number of microsites available for trees with similar canopy size would increase if the threshold value of PFD required by the trees decreases. Therefore, both PFD and space availabilities must be considered in the estimation of microsites utilized for the establishment of tree seedlings within grass canopies. Further data between transects would give a better understanding of the two-dimensional characteristics of microsites in contour maps. However, it was technically difficult to obtain such data because of the artificial disturbance during the light measurement. An alternative approach is to obtain more information from the transect data.

Examination of the PFD-available spans from the transect data provided a good insight into the importance of spatial dimension of microsites (Fig. 7). A large proportion of PFD-available spans with a distance shorter than 8 cm suggests that such small spans may spatially limit those seedlings with a crown larger than 8 cm in diameter.

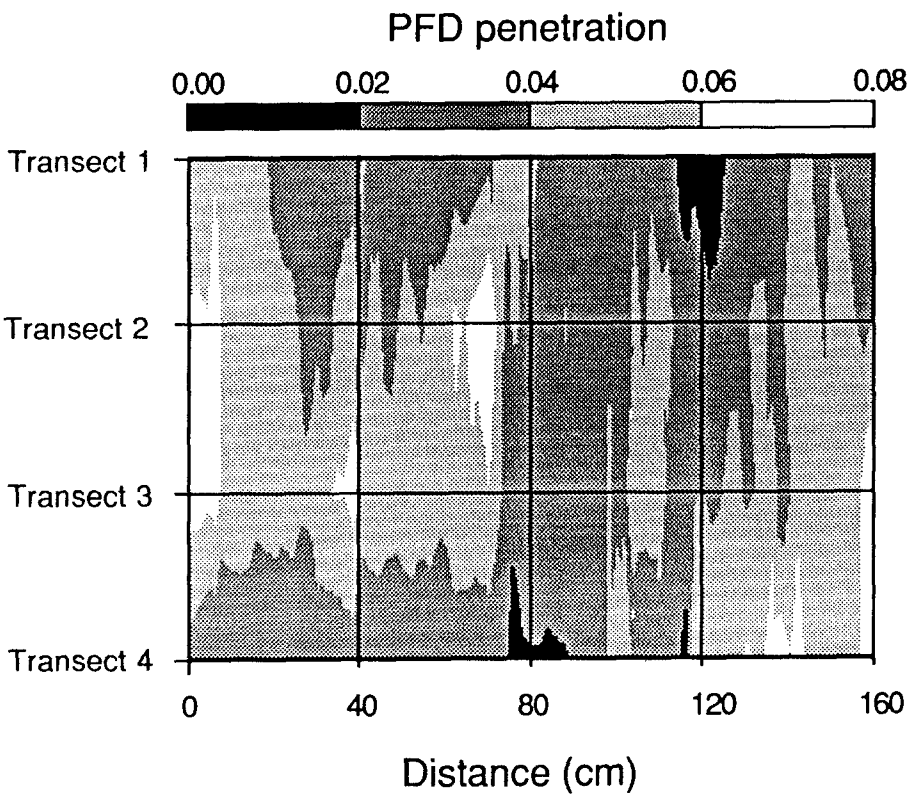

Fig. 8. A contour map for PFD penetrations within a *M. sinensis* canopy. Different PFD penetrations were indicated by different line patterns. The data were the same as in Fig. 2.

When 2000 μmol m^{-2} s^{-1} PFD is recorded above a canopy under clear skies, a difference of 0.01 PFD penetration means a variation of 20 μmol m^{-2} s^{-1}. The present study indicates that at least 18% of neighbor points along the transects have difference of 0.01 penetration, therefore, these points would have a PFD difference above 20 μmol m^{-2} s^{-1} between 2 cm under a clear sky condition (Fig. 5). Since one-dimensional size of a single leaf in tree seedlings would be larger than 2 cm in general, considerable within-leaf variation in PFD would occur under clear sky conditions. Such within-leaf or within-individual variations might have an important ecophysiological significance. In the lower canopy layers of a dense grass, PFD was usually lower than 50 μmol m^{-2} s^{-1}, which is close to the compensation PFD of photosynthesis for most heliophilic tree species (Pearcy 1990; Tang *et al.* 1992a). Around the compensation PFD, a slight increase in PFD has a large effect on photosynthesis because of the linear relationship between photosynthesis and PFD. Therefore, photosynthesis might not be uniform within a leaf due to the heterogeneity of PFD. Further studies are needed to reveal the relationship between the small-scale heterogeneity of PFD and physiological process of photosynthesis within a single leaf.

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