Analysis of leaf arrangement and light penetration in a Japanese cypress seedling population by the point quadrat method

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ポイント法によるヒノキ苗個体群の葉の配列と光透過の解析

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Leaf arrangement and light penetration in a 2-year-old seedling population of *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. were investigated by using the point quadrat method. Long needles, or point quadrats, were placed vertically through the seedling canopy. The leaves were clumped in layers excluding the uppermost layer where they were distributed at random. The proportion of quadrats making no contacts to the total number of quadrats can be considered to correspond to the proportion of light penetrating through the canopy, on the supposition that the sunlight ray is vertically incident on the canopy and its diffusion and transmission by leaves are ignored. The proprotion $p(z)$ decreased with the mean number of increasing contacts per quadrat $f(z)$ from the canopy surface down to a depth z, which followed an exponential function, viz. $p(z) = \exp(-k \cdot f(z))$. The constant k was estimated to be 0. 47 in November 1981, 0.54 in June, and 0.61 in September 1982. The constant tended to increase with the canopy development.

ポイント法を用いて，岐阜営林署緑ケ丘種苗事業所（岐阜県美濃加茂市）内の苗畑に生育するヒノキ苗個体群（1980年３月播種，翌年３月床替え）の葉の配列と葉群内の光透過について研究した。測定は1981年11月と翌年の６月，９月に行った。光の入射方向が垂直であると仮定して，ステンレス製の針（直径1.5 mm，長さ１ m）を樹冠内に垂直に挿入し，針と葉との接触数を層別に記録した。観測度数は250～1000であり，針は毎回ランダムに樹冠内に挿入された。針と葉との接触数の頻度分布から葉の空間配列に集中性が認められた。接触数０の割合は，葉による光の透過，散乱を無視すれば葉群内における光の透過率とみなせる。樹冠表面から深さ z までの接触数０の割合を $p(z)$，z までの接触数の平均値を $f(z)$ とすると，両者の間には $p(z)=\exp(-k \cdot f(z))$ が成立した。係数 k の値は，６月が0.47，９月が0.54，11月が0.61と計算され，生長とともに増加する傾向を示した。

Key words: *Chamaecyparis obtusa*; Leaf arrangement; Light penetration; Point quadrat method; Seedling population.

I. Introduction

Analysis of leaf canopy structure is indispensable for estimating photosynthetic production in a plant population, as the canopy structure is closely related to the process of light penetration (Monsi and Saeki 1953). In order to assess the canopy structure in grasslands, Warren Wilson (1959a, b) developed the point quadrat method.

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Point quadrats inclined at a particular angle to the horizon can give information on the interception of light entering at the same inclination (Warren Wilson 1965). Ford and Newbould (1971) applied the point quadrat method to a forest composed of sweet chestnut trees.

In this paper, leaf arrangement was investigated by employing the point quadrat method as part of a series of studies on a seedling population of *Chamaecyparis obtusa* (Ogawa et al. 1985, 1986). Moreover, the process of light penetration inside the seedling canopy was examined on an assumption that light came vertically from the sky and its scattering and transmission by leaves could be ignored.

II. Materials and Methods

This experiment was conducted on November 25, 1981 and June 22 and September 21, 1982 on a seedling population of Japanese cypress, *Chamaecyparis obtusa* (Siebold & Zucc.) Endl., growing in Midorigaoka Nursery at Minokamo of the Gifu District Forest Office, Gifu Prefecture. Seeds were sown in March 1980 and the seedlings were transplanted in March 1981. The seedling density was 62 m^{-2}. General features of the seedling population are summarized in Table 1.

By inserting vertically a stainless needle (1.5 mm in diameter and 1 m in length) into the seedling canopy at random, the number of contacts of the needle with the leaves was recorded. The records were made at intervals of 4 cm on November 25 and June 22, and 6 cm on September 21 from the canopy surface to the ground. The number of point quadrats was 250 on November 25, 1000 on June 22, and 500 on September 21.

III. Results and Discussion

1. *Leaf arrangement*

If light is vertically incident on the seedling canopy, the light penetration inside the canopy depends on the dispersion of the area of leaves projected on the horizon. The dispersion is assessed by the variability of the point quadrat scores, which can be expressed as the ratio of the variance to the mean of the number of contacts per quadrat (Warren Wilson 1959a). This ratio, the relative variance, is equal to one for random, is greater than one for clumped, and is less than one for reqular arrangements.

Figure 1 shows the frequency distribution of the number of contacts per quadrat when the point quadrats passed through the full depth of the canopy. The number of contacts per quadrat is equivalent to a leaf area index in vertical projection. The frequency distribution showed a typical

Table 1. General features of the seedling population.

Date	H	H_B	D_0	D_B	$D_{0.1}$	y
			[cm]			[kg m^{-2}]
Nov. 25, 1981	26.7	1.7	0.44	0.41	0.40	0.43
Jun. 22, 1982	36.9	2.1	0.57	0.53	0.50	0.71
Sep. 21, 1982	51.1	2.4	0.69	0.63	0.59	1.24

The symbols H, H_B, D_0, D_B, $D_{0.1}$, and y stand for the mean of seedling height, clear length, diameter at ground surface, diameter at the clear length, and diameter at one-tenth of the seedling height, and biomass (dry), respectively.

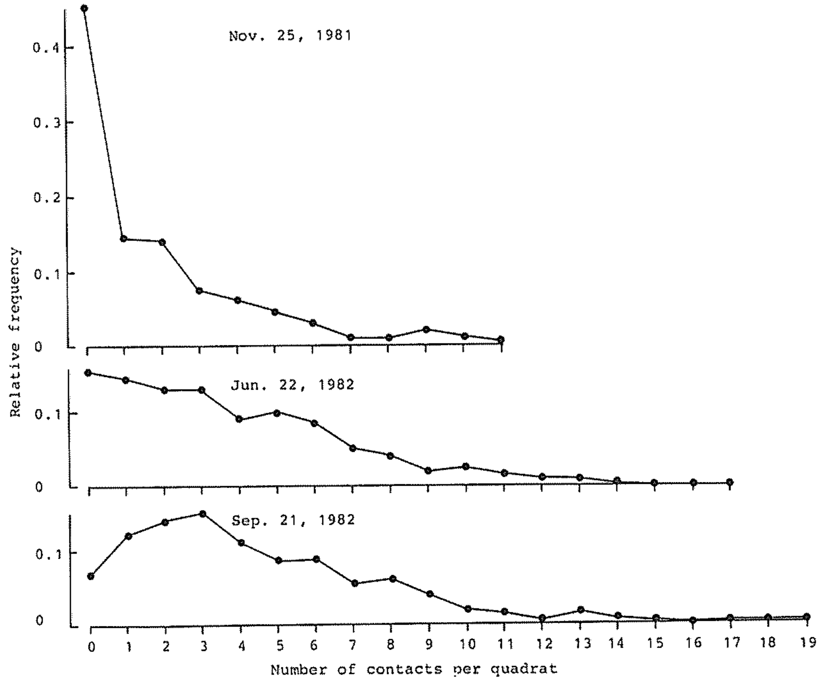

Fig. 1. Frequency distribution of the number of contacts per quadrat penetrating full depth of the seedling canopy. The number of contacts per quadrat is equal to a leaf area index in vertical projection.

Table 2-A. Mean m, variance s^2, and relative variance s^2/m of number of contacts for point quadrat data on November 25, 1981.

Height interval cm-cm	Each layer			Cumulative layer		
	m	s^2	s^2/m	m	s^2	s^2/m
28−32	4.00(−3)	3.98(−3)	1.00	4.00(−3)	3.98(−3)	1.00
24−28	2.40(−2)	3.14(−2)	1.31**	2.80(−2)	4.32(−2)	1.54**
20−24	1.32(−1)	2.35(−1)	1.78**	1.60(−1)	3.26(−1)	2.04**
16−20	3.00(−1)	6.10(−1)	2.03**	4.60(−1)	1.15	2.51**
12−16	4.40(−1)	7.26(−1)	1.65**	9.00(−1)	2.63	2.93**
8−12	4.56(−1)	7.20(−1)	1.58**	1.36	4.05	2.99**
4− 8	3.56(−1)	5.41(−1)	1.52**	1.71	5.38	3.14**
0− 4	5.60(−2)	6.89(−2)	1.23**	1.77	5.68	3.21**

The significance of departure from the value of one is indicated by ** for the level 0.01. Figures in parentheses denote an exponent with the base 10. Total number of quadrats : 250.

Table 2-B. Mean m, variance s^2, and relative variance s^2/m of number of contacts for point quadrat data on June 22, 1982.

Height interval cm-cm	Each layer			Cumulative layer		
	m	s^2	s^2/m	m	s^2	s^2/m
52−56	1.00(−3)	9.99(−4)	1.00	1.00(−3)	9.99(−4)	1.00
48−52	0.00	0.00	−	1.00(−3)	9.99(−4)	1.00
44−48	7.00(−3)	6.95(−3)	0.99	8.00(−3)	7.94(−3)	0.99
40−44	3.60(−2)	4.87(−2)	1.35**	4.40(−2)	5.81(−2)	1.32**
36−40	7.30(−2)	9.17(−2)	1.26**	1.17(−1)	1.65(−1)	1.41**
32−36	1.35(−1)	2.09(−1)	1.55**	2.52(−1)	4.50(−1)	1.79**
28−32	1.98(−1)	2.67(−1)	1.35**	4.50(−1)	8.58(−1)	1.91**
24−28	3.02(−1)	4.45(−1)	1.47**	7.52(−1)	1.60	2.13**
20−24	4.83(−1)	7.44(−1)	1.54**	1.24	2.77	2.24**
16−20	6.34(−1)	8.36(−1)	1.32**	1.87	4.26	2.28**
12−16	7.35(−1)	9.65(−1)	1.31**	2.60	6.09	2.34**
8−12	6.29(−1)	8.87(−1)	1.41**	3.23	8.16	2.53**
4− 8	3.81(−1)	5.76(−1)	1.51**	3.61	9.54	2.64**
0− 4	7.90(−2)	1.15(−1)	1.45**	3.69	9.94	2.69**

Total number of quadrats : 1000.

Table 2-C. Mean m, variance s^2, and relative variance s^2/m of number of contacts for point quadrat data on September 21, 1982.

Height interval cm-cm	Each layer			Cumulative layer		
	m	s^2	s^2/m	m	s^2	s^2/m
78−84	2.00(−3)	2.00(−3)	1.00	2.00(−3)	2.00(−3)	1.00
72−78	8.00(−3)	7.94(−3)	0.99	1.00(−2)	9.90(−3)	0.99
66−72	2.80(−2)	3.52(−2)	1.26**	3.80(−2)	5.66(−2)	1.49**
60−66	6.20(−2)	1.30(−1)	2.10**	1.00(−1)	2.62(−1)	2.62**
54−60	1.30(−1)	2.09(−1)	1.61**	2.30(−1)	5.53(−1)	2.41**
48−54	2.08(−1)	2.53(−1)	1.22**	4.38(−1)	1.08	2.46**
42−48	2.46(−1)	3.73(−1)	1.52**	6.84(−1)	1.90	2.78**
36−42	3.66(−1)	4.72(−1)	1.29**	1.05	2.89	2.75**
30−36	4.84(−1)	5.38(−1)	1.11**	1.53	3.92	2.56**
24−30	5.82(−1)	6.51(−1)	1.12**	2.12	5.19	2.45**
18−24	5.74(−1)	6.69(−1)	1.17**	2.69	6.50	2.42**
12−18	9.12(−1)	1.08	1.18**	3.60	8.52	2.36**
6−12	6.58(−1)	8.45(−1)	1.28**	4.26	1.06(+1)	2.48**
0− 6	1.68(−1)	2.64(−1)	1.57**	4.43	1.15(+1)	2.59**

Total number of quadrats : 500.

L-shape on November 25, 1981. The relative frequency of quadrats with no contacts decreased with the seedling growth. The mode of the frequency distribution transferred to three on September 21, 1982. As given in Table 2, the relative variance of a set of point quadrats in Figure 1 was calculated at 3.21 on November 25, 2.69 on June 22, and 2.59 on September 21. These values differed significantly from one ($P<0.01$), indicating clumping of foliage. Thus, in some places leaves were in heavy shade while in other places strong light fell on the ground. However, it is noted that the leaves were randomly dispersed in the uppermost layers.

2. Light penetration

Figure 2 depicts the mean number of contacts per unit length of point quadrat within successive layers. The mean number of contacts in a given layer stands for the area density of leaves projected on the horizon. The skewness, a measure of

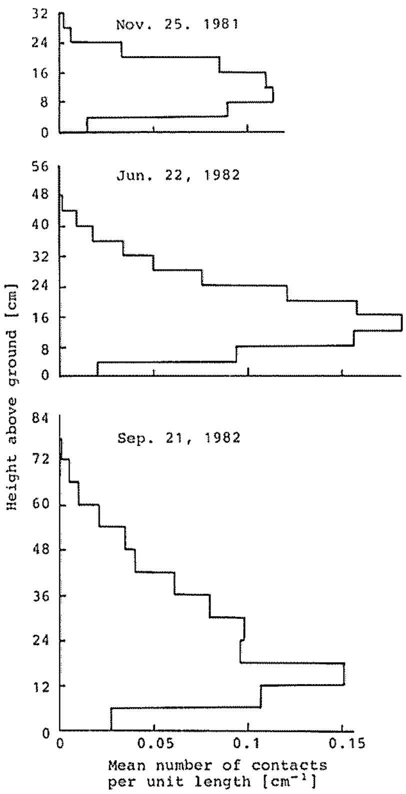

Fig. 2. Mean number of contacts per unit lenght of point quadrat within successive layers. The mean number of contacts represents the area density of leaves projected vertically on the horizontal plane.

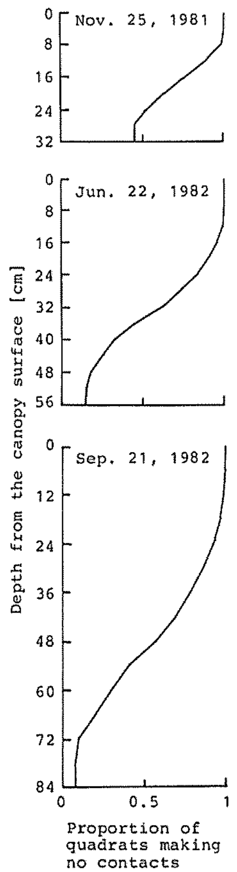

Fig. 3. Proportion of quadrats making no contacts from the canopy surface down to a depth. When vertical light beams are assumed and the scattering and transmission of light by leaves are to be neglected, the proportion corresponds to that of light penetrating through gaps in the leaves.

asymmetry of distributions, was determined to be 0.33 in November 25, 0.65 in June 22, and 0.72 in September 21. This change in the skewness means that the vertical distribution tended to tail toward the upper layers with the canopy development.

The proportion of quadrats making no contacts to the total number of quadrats from the canopy surface down to a depth is exhibited in Figure 3. The proportion is equal to the proportion of light penetrating through gaps in the canopy to light vertically incident on the canopy surface. Its value decreased with increasing depth from the canopy surface. The amount of light reaching the ground reduced with the canopy development.

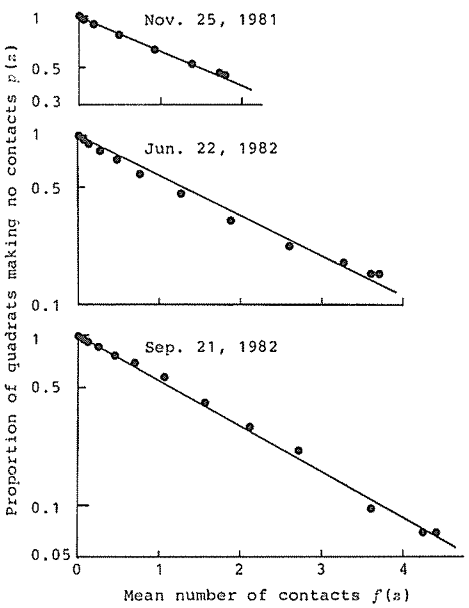

Fig. 4. Relationship between the proportion of quadrats making no contacts $p(z)$ and the mean number of contacts per quadrat $f(z)$ from the canopy surface down to a depth z. The straight lines are an approximation based on Eq. (1). The constant k in Eq. (1) was calculated at 0. 47 on November 25, 0. 54 on June 22, and 0. 61 on September 21.

The proportion of making no contacts $p(z)$ from the canopy surface down to a depth z is plotted against the mean number of contacts per quadrat $f(z)$ between the depth and the canopy surface, as shown in Figure 4. The functions of $p(z)$ and $f(z)$ can be respectively regarded as the relative illuminance at a depth z from the canopy surface and the vertically projected area of leaves existing from the canopy surface to the depth. The relationship between the two quantities was approximated by the following exponential function:

$$p(z)=\exp(-k\cdot f(z)), \quad (1)$$

where k is a constant specific to each season. The value of k was calculated at 0.47 on November 25, 0.54 on June 22, and 0.61 on September 21. Therefore, the value tended to increase with the canopy development.

The constant k in Eq. (1) was below unity for all observations. This is considered to result from clumped leaf dispersion observed in layers except for the uppermost ones with a small amount of leaves, taking account of the model proposed by Acock et al. (1970).

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