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Modelling the relationship between the asymmetry in crown display and local environment

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Twenty-eight text pages (including a table and two figure
legend) and five figures.

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ABSTRACT

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The asymmetry in crown display was modeled with respect to neighbors and microtopography. The direction and magnitude of the asymmetry were expressed by the 'crown-vector', the horizontal two-dimensional vector that joins the stem base position of a focal tree with the centroid of its projected crown area. In the model, the crown-vector of a focal tree was a function of the position and size of its neighbors and the direction and inclination of the slope on which it occurred.

Using the model, the effect of repelling behavior of crowns on the spatial pattern of crowns was quantified; spatial patterns of crowns were more regular than those of stem bases. The effects of parameters in the model on the spatial pattern of population were also quantified.

The model was applied to the data derived from two study plots: one in cool temperate deciduous broad-leaved forest in northern Japan and the other in warm temperate evergreen broad-leaved forest in central Japan. The least-squares fit of the model accounted for 56% and 73% of the total variance in crown-vector for the two study plots, respectively.

INTRODUCTION

The plasticity in crown shape of individual trees has been reported in relation to the quantity and quality of light (Koike, 1986; Ballaré et al., 1988; Koike et al., 1990). If the light environment around a tree is horizontally heterogeneous, the plant has an asymmetric crown through differential growth of module populations in the crown (Jones, 1985; Franco, 1986; Solangaarachchi and Harper, 1989; Novoplansky et al., 1990). This asymmetry can be considered adaptive, because plants can place their foliage in the favorable space where they can intercept more light.

The asymmetry affects not only an individual's performance but also phenomena at the population and community levels. For example, asymmetry can modify the size distribution of a population through changes in the growth of individuals (Sorrensen-Cothorn et al., 1993) and spatial structure in community (Ishizuka 1984). It also can affect gap dynamics because the unbalanced crown distribution reduces the mechanical stability of trees (Young and Hubbell, 1991).

Sorrensen-Cothorn et al. (1993) developed an elaborate competition model incorporating crown plasticity, and showed that asymmetry in crown display is important for the growth and structure of tree populations. In their model, the asymmetry in crown display is described as three-dimensional distribution of foliage in an individual tree, not with simple parameters such as circular statistics (Franco, 1986; Solangaarachchi and Harper, 1989). Their model also includes parameters that determine the growth and survivorship of branches (sectors of whorls, in their model)

such as sector increment rate or minimum production required to sustain a sector. The complexity of the expression of the asymmetry, together with the necessity of demographic parameters of modules, makes it difficult to calibrate their model in the field for summarizing the morphological plasticity of crowns.

On the other hand, the asymmetry in crown display has been described with simple parameters (Takiguchi, 1983; Franco, 1986; Solangaarachchi and Harper, 1989; Young and Hubbell, 1991). These parameters, however, have not been modeled as functions of the local environment of single trees. If these simple parameters are modeled as functions of the local environment, we can easily use these models to summarize the morphological plasticity of crowns by calibrating them in the field.

'Crown-vector' is one of the simple parameters that can express the asymmetry in crown display (Takiguchi, 1983). It is the two-dimensional vector that joins the stem base position of an individual plant with the centroid of its projected crown area (Fig. 1a). If the crown-vector is modeled as a function of the local environment of single trees, we can predict the position of the centroid of projected crown area (hereafter, crown center) from the position of stem base and the local environment. Because mainly crowns modify the light environment in communities, crown center is the most appropriate point that represents an individual plant from the viewpoint of its effect on light. Usually the positions of crown centers are different from the stem base positions because of plasticity in crown

shape (Ishizuka, 1984). In many neighborhood interference models, stem base position is used as the representative point of an individual plant (Mack and Harper, 1977; Weiner, 1982, 1984; Biging and Dobbertin, 1992; Silander and Pacala, 1985; Watkinson et al., 1983; Mithen et al., 1984).

However, if interactions between individuals are mediated by light, crown center should be used as the representative point of an individual. If we can predict the positions of crown centers and use them instead of the stem base positions, we can incorporate crown plasticity into neighborhood interference models. By incorporating crown plasticity into neighborhood interference models, we also can evaluate how adaptive the asymmetry is for an individual's performance or how the asymmetry might affect the dynamics of population or community without detailed demographic information about modules.

In this paper (1) a model, in which the crown-vector of an individual is a function of its local environment, is proposed, (2) using computer-generated populations, the effect of crown asymmetry on the spatial structure of the populations is clarified, and (3) the characteristics in crown plasticity in two different forest stands are discussed from the results of applications of the model.

THE MODEL

Crown-vector

Crown-vector is the two-dimensional vector that joins the stem base position of an individual plant with its crown center (Fig. 1a). The direction and magnitude of the asymmetry in crown display can be expressed using the crown-vector. It can express the mean deviation of the crown from the stem base position, regardless of the size of crown or tree height. In measuring the crown-vector, the crown of a tree occurring on a slope should be projected on the horizontal plane. The crown-vector, therefore, lies on the horizontal plane, not on the slope (Fig. 1b).

Model Description

The model is expressed as the product of two components: one indicates the influence of environment (G) and the other the response of focal trees to the influence of environment (F);

$$C = F(\text{focal tree}) G(\text{environment}) + e, \quad \text{< equation 1 >}$$

where C is the crown-vector, and e is an error vector.

Function F is assumed to be size-dependent;

$$F(\text{focal tree}) = c_0 H^l, \quad \text{< equation 2 >}$$

where H is the height of a focal tree, c_0 and l are constants. This is the same mathematical expression as that of allometry. The parameter l indicates how the plastic

response of the focal tree depends on its height. For example, when h is one, the response is proportional to tree height, and when h is zero, is identical in their magnitude, irrespective of tree height. The parameter c_0 also determines the magnitude of the response. It cannot be estimated in calibration because it is multiplied by other constants in the whole model as mentioned below.

Two tendencies are often observed in the crown display. First, when trees occur close to one another, they repel each other in their crowns (Jones, 1985; Young and Hubbell, 1991). Second, if a tree occurs on a slope, it shifts its crown toward the lower side of the slope (Hallé et al., 1978). The second component of the model (G), therefore, consists of these two elements: 1. the neighbor term, 2. the microtopography term. These terms are assumed to be additive. Thus the second component (G) is expressed as:

$$G(\text{environment}) = c_1 \cdot E_1 + c_2 \cdot E_2, \quad < \text{equation 3} >$$

where E_1 and E_2 denote two-dimensional vectors that indicate the neighbor term and microtopography term, respectively, and c_1 and c_2 are constants. The neighbor term E_1 can be expressed as:

$$E_1 = \sum_i \frac{h_i^m}{d_i^n} u_i, \quad < \text{equation 4} >$$

where h_i is the height of the i -th neighbor, d_i is the distance between the stem base position of the focal tree and that of the i -th neighbor, and m and n are parameters to

be determined in applications. The effect of the j -th neighbor on the crown-vector of a focal tree is assumed to have the direction from the stem base position of the neighbor to that of the focal tree; u_j is the horizontal unit vector giving the direction from the stem base position of the j -th neighbor to that of the focal tree. The mathematical expression of the magnitude of the effect of a neighbor on a focal tree (i.e. $\frac{h_j^m}{d_j^n}$) is similar to that of some neighborhood interference models (Weiner, 1984; Fowler, 1984; Firbank and Watkinson, 1987; Thomas and Weiner, 1989). It is, however, different from that of the previous models in that the exponents of the denominator and the numerator are not definite constants, but model parameters to be estimated. It must be noted that the effects of different neighbors should be added as vectors, not as scalars (Fig. 2).

The microtopography term can be expressed as:

$$E_2 = \alpha v, \quad \text{< equation 5 >}$$

where α is the inclination of the slope on which the focal tree occurs and v is the horizontal unit vector giving the direction of the steepest inclination of the slope.

After substitution of equation 2-5, equation 1 can be expanded as:

$$C = a \cdot T_1 + b \cdot T_2 + e, \quad \text{< equation 6 >}$$

where $T_1 = H^1 \cdot \sum_i \frac{h_i^m}{d_i^n} u_i$ (neighbor predictor), $T_2 = H^1 \cdot \alpha v$ (microtopography predictor), $a=c_0 c_1$, and $b=c_0 c_2$.

Goldberg (1990) divided the indirect interactions between individual plants into two components: the effect of plants on resources and the response of plants to the changed resources. The two components in the model described above (E and G) correspond to the components in her discussion; Neighbors and slope determine the gradient in light and plants respond to the gradient in terms of asymmetric crown display. In the model, both effect and response of individual plants are assumed to be size-dependent; the effect and response have allometric relations to height with exponents m and n , respectively. Thus, various patterns of interactions can be expressed with different combinations of n and m . For example, when n is zero and m is one, neighbors have effect proportional to their height and focal individuals respond irrespective of their height. In this situation, the interaction between individuals is similar to relative-size symmetry in competitive interactions (Weiner 1990). When n is zero and m is larger than one, the interaction in terms of crown shape is similar to asymmetry (but not absolute asymmetry) in competitive interactions. However, the interaction in terms of crown shape is different from competitive interactions in that the former is positive (the presence of neighbors increases the asymmetry in crown shape of a focal tree), whereas the latter is negative (the presence of neighbors reduces the growth of a focal tree). They are also different in that

effect of neighbors is directional in the former, whereas non-directional in the latter.

EFFECT OF THE PLASTICITY ON SPATIAL PATTERN

In the model, crowns repel each other so that spatial patterns of crowns are expected to differ from those of stem bases. To quantify to what extent the spatial pattern can change through the plasticity in crown shape and how parameters in the model affect the spatial patterns, I calculated the spatial pattern of stem bases and crown centers in computer-generated populations.

Methods

Five hundred individuals were located in a 60 × 60 square randomly. A number derived from normal distribution with a mean of 12 and standard deviation 5 was given to each individual as its height. Using the model, I calculated crown-vectors which determine the positions of crown centers. If the slope on which the population occurs is flat, the microtopography predictor (T_2) in equation 6 can only shift crowns in the fixed direction of the steepest inclination of the slope to the extent related to individual's height; it cannot affect spatial pattern. The microtopography predictor (T_2) was, therefore, neglected. I set λ , μ , and α at unity as the baseline combination of parameters, and changed one of three parameters in turn to clarify the effect of each parameter. In total, seven different patterns of crown centers were calculated for one population, corresponding to seven combinations of parameters. Parameter α was so adjusted that the mean magnitude of crown-vectors was 2.5. The mean and standard deviation of height, density of individuals, and the mean

magnitude of crown-vectors were set so that they were similar to those of data sets to which I applied the model below. I employed Hopkins' Index (Diggle, 1983) to quantify spatial pattern. Hopkins' Index is given by

$$HI = \frac{\sum x_i^2}{\sum x_i^2 + \sum y_i^2},$$

where HI is Hopkins' Index, x_i denotes the distance from i -th random point in the population to the nearest neighbor, and y_i the distance from i -th randomly sampled individual to the nearest neighbor. Summations are over $i=1, \dots, m$, where m is the number of sampling points (random points or randomly sampled points). I adopted 100 as m . Hopkins' Index ranges from zero to one, and indicates that individuals are aggregated when it is more than 0.5 and regular when it is less than 0.5. I calculated Hopkins' Index from the locations of crown centers and stem bases for all individuals and three height classes (large, medium, and small) separately. Individuals outside the 36×36 square in the center of the plot were excluded from calculations to minimize the edge effect. One hundred replications (populations) were generated and mean values of Hopkins' index were calculated.

Results

Figure 3 shows an example of crown-vectors in a computer-generated population (In the figure, the 10×10 square in the center of the whole population is shown). Crown-vectors are expressed by arrows whose bases and points indicate the

stem bases and crown centers, respectively. Crowns are shown by circles whose radius is proportional to individual's height. Crown-vectors whose bases are close to one another tend to point at opposite direction of each other.

The spatial patterns of crown centers generally became more regular than those of stem bases (Fig. 4a-4d); one exception was the case with parameter n being zero in which the model did not consider the effect of distance between the stem base position of the focal tree and that of the i -th neighbor (the effect of a neighbor did not decrease with the distance from the neighbor). This change in spatial pattern is important for population dynamics, because it can reduce competition in a population. Ishizuka (1984) calculated the spatial patterns of crown centers and stem bases in forest communities, and found that the spatial patterns of crowns were more regular than those of stem bases. He speculated that the regular spatial patterns of crowns developed through competition among individuals. The results presented here can support his speculation.

The effect of crown plasticity on the spatial patterns of crown centers varied in strength for different height classes; it was strongest for large individuals, and weakest for small individuals. This is because of the positive values for parameters l and m . If l and m are negative, opposite trends can be observed.

Although the general patterns of the change in spatial patterns for large individuals (Fig. 4b) were similar to those for all individuals (Fig. 4a), there were some

differences. For example, there was an opposite trend in spatial patterns in relation to parameter μ (See the 5th-7th columns from left). For all individuals, the effect of crown plasticity was strongest if μ was zero, whereas, for large individuals, it was strongest if parameter μ was three. This means that, if the repelling effect between crowns is independent of the size of individuals (μ is zero), crown plasticity changes the spatial pattern so that crowns of all individuals are placed regularly, while, if the repelling effect of larger individuals is disproportionately strong (μ is larger than one), crown plasticity has the effect that makes the spatial patterns of crown centers of larger individuals regular.

APPLICATIONS

Data collection

Two 25 m $\times$ 25 m plots were established to collect data for estimating model parameters: one (hereafter, plot D) in cool temperate deciduous broad-leaved forest in Hokkaido, northern Japan, and the other (hereafter, plot E) in warm temperate evergreen broad-leaved forest near Kyoto, central Japan. Plot D was dominated by *Betula Maximowicziana*, an early successional species in cool-temperate forests, and plot E by *Castanopsis cuspidata*, a representative climax species in warm-temperate forests in Japan. The canopy heights in plot D and E were about 25 m and 20 m, respectively. Both plots were established in mature stands without distinct canopy gaps.

In each plot, the heights of the trees greater than 4.0 cm in diameter at breast height were measured. Crown projection maps were drawn and crown centers were determined by cutting outlines of projected crowns and suspending each from multiple pivot points. Microtopography was measured with a surveying compass (TRACON s-25 Ushikata Mfg. co., ltd. Tokyo Japan). Each plot was divided into 100 small triangles, and the inclinations and aspects of these triangles were calculated. The trees outside the 15 m $\times$ 15 m square in the center of each plot were eliminated from the population of focal trees and used as neighbors only to avoid the error due to plot margin. Trees that were apparently injured by other physical factors were also eliminated from analysis.

Calibration of the model

For calibration, equation 6 is divided into two elements:

$$C_x = a \cdot T_{1x} + b \cdot T_{2x} + e_x$$

$$C_y = a \cdot T_{1y} + b \cdot T_{2y} + e_y ,$$

where $C=(C_x, C_y)$, $T_1=(T_{1x}, T_{1y})$, $T_2=(T_{2x}, T_{2y})$, and $e=(e_x, e_y)$. Subscripts x and y indicate orthogonal directions on the horizontal plane. Because they are independent of each other, we do not have to make a distinction among them. We can, therefore, treat them in the same manner. Accordingly, we can translate the model into a scalar model:

$$C = a \cdot T_1 + b \cdot T_2 + e. \quad < \text{equation 7} >$$

If the parameters $\underline{l}$, $\underline{m}$, and $\underline{n}$ are given, $\underline{a}$ and $\underline{b}$ can be calculated by the multiple regression method. I used the statistic $r^2 = 1 - \sum (C - \hat{C})^2 / \sum (C - \bar{C})^2$ (the coefficient of determination) to evaluate the fit of the model. Although many alternative r^2 statistics have been proposed, the above r^2 statistic ought to be used especially in cases where regression models do not include the intercept (Kvålseth, 1985). For each data set, I tried various integer combinations systematically on a computer, searching for the best values for $\underline{l}$, $\underline{m}$, and $\underline{n}$, with which the coefficient of determination was maximum. In total, five parameters ($\underline{a}$, $\underline{b}$, $\underline{l}$, $\underline{m}$, and $\underline{n}$) were estimated in each calibration.

To evaluate the relative strength of the two explanatory variables T_1 and T_2 , parameters $\underline{a}$ and $\underline{b}$ were standardized as:

$$a' = a \frac{s_{T_1}}{s_C}$$

and

$$b' = b \frac{s_{T_2}}{s_C},$$

where s_C , s_{T_1} , and s_{T_2} denote the standard deviation of C , T_1 , and T_2 , respectively. Standardized coefficients a' and b' give the rate of change in standard deviation units of the criterion variable (C) per one standard deviation unit of the explanatory variables T_1 and T_2 , respectively. These standardized coefficients can be compared directly with each other as the relative standardized strengths of the effects of explanatory variables on the same criterion variable.

Statistical Test

Since the neighbor predictors (T_1) are not independent of each other, we cannot use ordinary statistical tests based on independence and normality of variables (Fowler, 1984; Mitchell-Olds, 1987; Thomas and Weiner, 1989). To test the significance of the model and parameters a' and b' , I used Fisher's Method of Randomization, which provides a distribution-free test of association when variables are not independent (Sokal and Rohlf, 1981). For each fitting, a null distribution of coefficient of determination (r^2) of the model was generated by randomly assigning the observed criterion variables (C) to the observed pairs of explanatory variables (T_1 and T_2) using 3000 replications. The null

hypothesis in this case is that the elements of crown-vector are unrelated to the elements of the neighbor predictor or the microtopography predictor. For testing the significance of the standardized parameters $\underline{a}'$ and $\underline{b}'$, the same method was used.

Results

The model accounted for a large portion (56% and 73% for plot D and E, respectively) of the variance in crown-vector (Table 1). The parameter $\underline{a}'$ and $\underline{b}'$ were significantly different from those of null hypotheses for both plots. For both plots, $\underline{b}'$ was larger than $\underline{a}'$, indicating that slope was more important than neighbors in determining the asymmetry in crowns. Although estimated parameters $\underline{I}$ and $\underline{II}$ were the same for both plots, parameter $\underline{III}$ differed between plots; for plot D, it was three, and zero for plot E.

Figure 5 illustrates the sensitivity of the model to parameter changes. Coefficient of determination of the model responded most sensitively to parameter $\underline{I}$ and least sensitively to parameter $\underline{III}$.

DISCUSSION

The presented model explained a large portion of the variance in observed crown-vectors. From the results of the applications, we can summarize the observed morphological plasticity in crown shape in communities. The summarized characteristics of the morphological plasticity in the two study plots are as follows.

First, the effects of neighbors and slope were significant in determining the asymmetry in crown display of individuals (Table 1). The proximate mechanisms that relate crown shape to neighbors and slope are thought to depend on access to light. In natural forest, neighboring trees are the most important obstacles that reduce light intensity and change light quality (Harper, 1977; Endler, 1993). Thus the population of modules increases more vigorously in the opposite side of neighbors than the side facing to the neighbors, making the crown shape asymmetric (Jones, 1985). Microtopography can be thought to affect crown display through the similar mechanism as neighbors. For a tree on a slope, the crowns of neighbors in upper side of the slope are situated at higher position than those of the same-sized neighbors in lower side. The light environment for the tree is more favorable in the lower side than in the upper side. Consequently, its crown grows more rapidly in the lower side than in the upper side.

Second, slope was more important than neighbors for both plots (Table 1). The aspect of slope determines the average direction of the gradient in availability of light for individuals. On the other hand, the position and size of

neighbors determine fine scale heterogeneity in light environment around the individuals. The dominant individuals of the plots are broad-leaved, which have wide crowns. The average gradient made by slope can be important for such trees.

Third, the estimated values for parameters λ , μ , and η can show quantitatively how the interaction between individuals works in communities in terms of morphological plasticity. The estimated values for parameter λ and η were unity for both plots (Table 1). The magnitude of plastic response in crown display was linearly dependent on height, and the effect of a neighbor was inversely proportional to its distance. There was an interesting difference in estimated parameter μ between two study plots (Table 1). The large μ for plot D indicates that the effect of large neighbors is disproportionately strong. In this case, we can say that plasticity in crown display works to reduce the competition especially between large trees, taking the results of spatial patterns in computer-generated populations (Fig. 4) into considerations. On the other hand, the effect of neighbors is independent of their height in plot E. In this case, the effect of crown plasticity works to reduce the competition between all individuals. This argument is, however, tentative because parameter μ had a weak effect on the fit of the model for presented two applications, and estimations were not accurate.

In the presented model, the crown-vector, which links the stem base and the crown center, is related to the local environment of single trees with a simple equation.

Therefore, we can predict the position of crown center from the stem base position and the local environment. Crown center is the most appropriate point that represents an individual, when the effect of the individual on light environment around it is considered. The positions of crown centers are different from those of stem bases because of the asymmetry of crown display (Ishizuka, 1984). Many competition models, in which spatial information plays an important role, have been proposed to explain growth (Mack and Harper, 1977; Weiner, 1982, 1984; Biging and Dobbertin, 1992), survivorship (Silander and Pacala, 1985), and fecundity (Watkinson et al., 1983; Mithen et al., 1984) of individuals. In these models, the interference between individuals is dependent on the position of their stem base. If we use the position of crown center predicted by the model instead of the stem base position, we can incorporate the plasticity in crown display into these individual-based models without detailed demographic information of modules in individual trees.

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Table 1 Results of application of the model to the data from two plots. ***, ** and * indicate that the coefficient of determination or the parameter is significant by Fisher's Method of Randomization at 0.1%, 1% and 5% level, respectively.

Plot name	No. of analyzed trees	parameters					r^2
		a	b'	l	m	n	
D	31	0.25*	0.68***	1	3	1	0.56***
E	39	0.36**	0.92***	1	0	1	0.73***

Fig. 1. Schematic representation of crown-vector. (a) Crown-vector is the two-dimensional vector that joins the stem base position with the centroid of the projected crown area of an individual tree. (b) Crown-vector of a tree that occurs on a slope lies on the horizontal plane not on the slope.

Fig. 2. Summation of the effects of multiple neighbors on a focal individual. The effects ($E1$ and $E2$) of two neighbors ($N1$ and $N2$) on a focal individual (E) are summed up to be one vector (E). Note that the effects of neighbors are summed as vectors, not as scalars.

Fig. 3. Crown-vectors calculated in a computer-generated population. Crown-vectors are expressed by arrows whose bases and points represent stem bases and crown centers, respectively. Crowns are expressed by circles whose radius is proportional to plant height. In calculation of crown-vectors shown in this figure, the baseline combination of parameters ($l=1$, $m=1$, and $n=1$) was used. Only the 10×10 square in the center of the whole population (60×60) is shown. See text for details.

Fig. 4. Effects of asymetry of crown display on spatial patterns. The positions of crown centers are determined in 100 computer-generated populations, using the model with seven combinations of parameters shown below diagrams. I set the parameters $\underline{l}$, $\underline{m}$, and $\underline{n}$ at unity as the baseline combination (this appears three times in each diagram), and changed one parameter in turn. Means of Hopkins' index for all, large, medium and small individuals are shown in (a)-(d). Columns with the same letter do not differ significantly from each other at the 5% level by the Wilcoxon signed-rank test. See text for details.

Fig. 5. Coefficients of determination for the model with different parameter values. Parameters $\underline{l}$, $\underline{m}$, and $\underline{n}$ are changed (± 2) from the best-fit combinations for each application. Arrows in diagrams indicate the best-fit combinations of parameters.

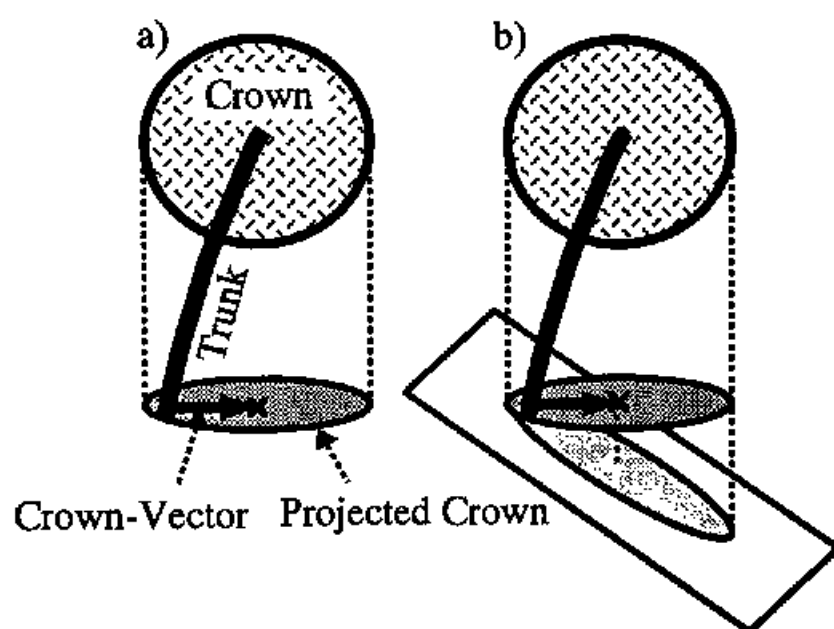


Fig. 1

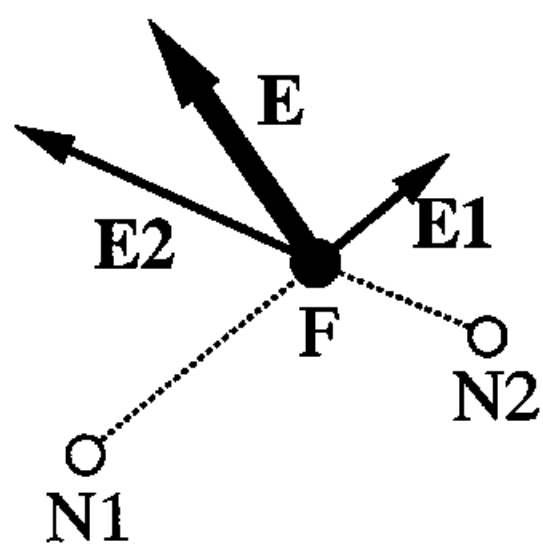


Fig. 2

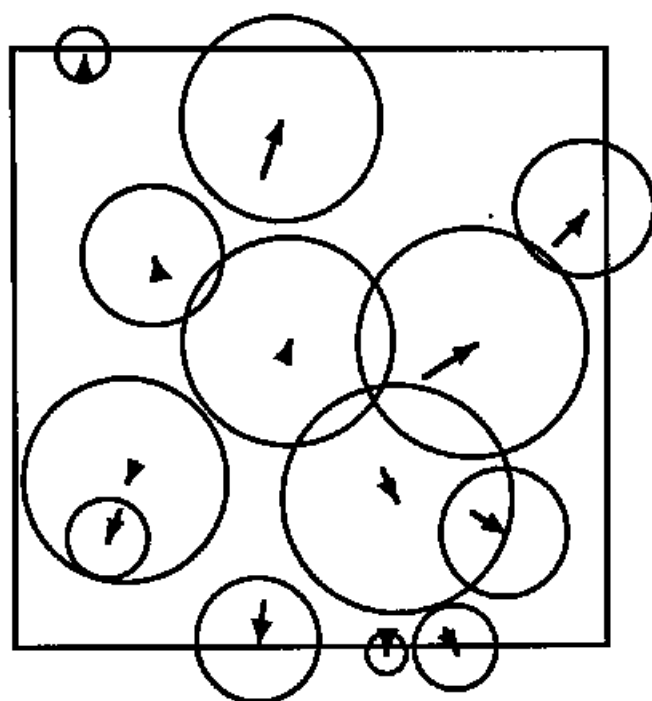


Fig. 3

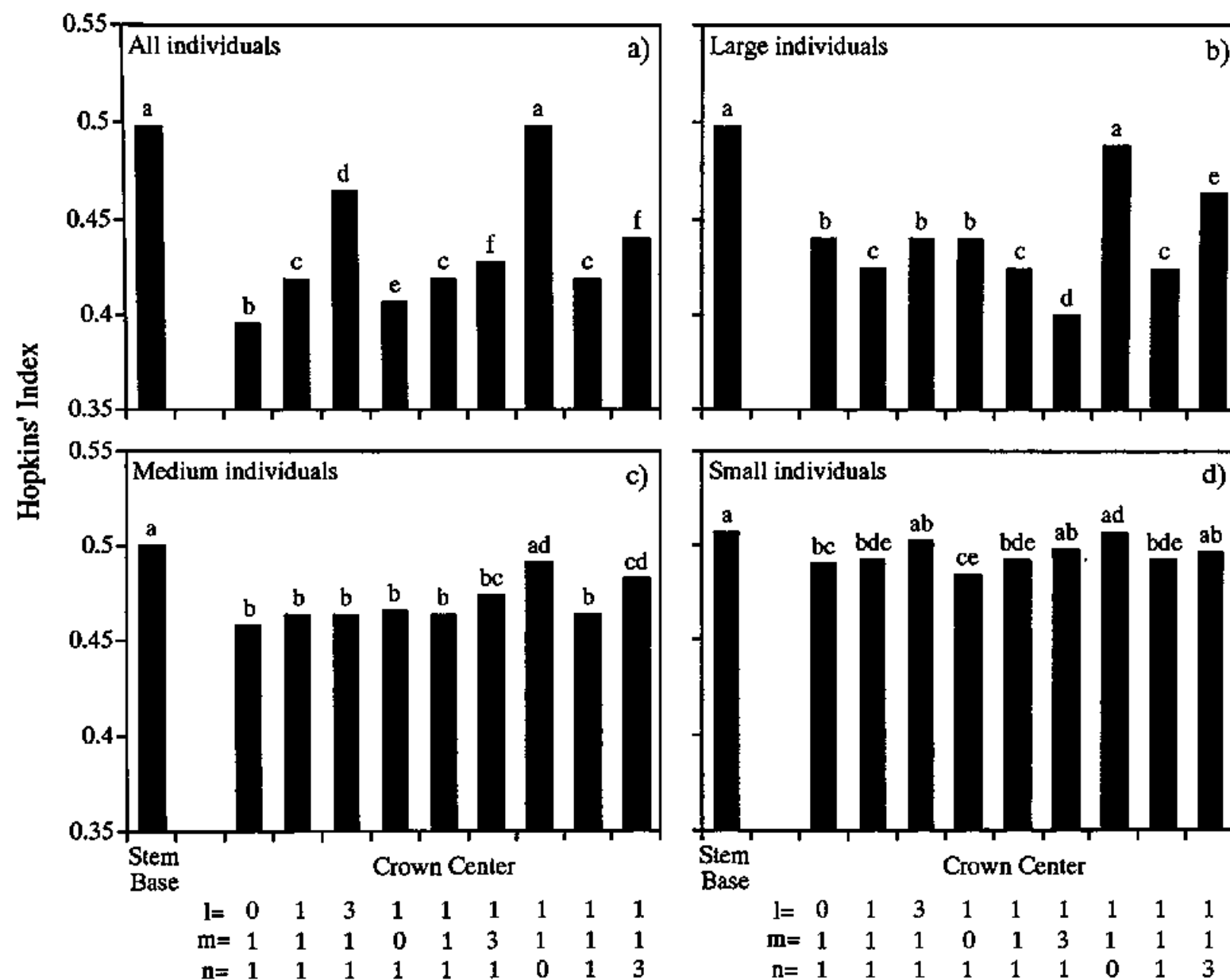


Fig. 4

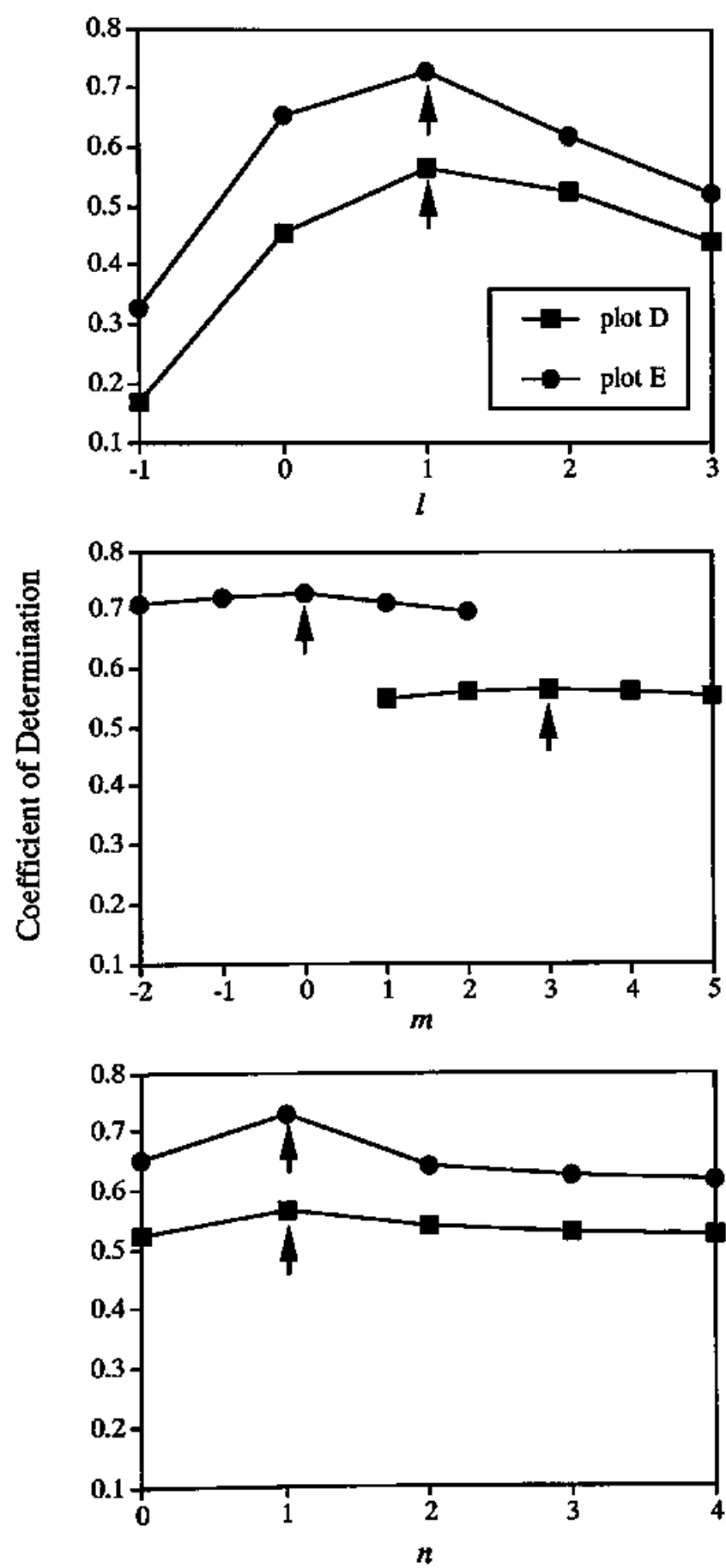


Fig. 5

ECOLOGICAL MODELLING

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Hokkaido Forestry Research Inst.
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Re.: ECOMOD 1033

Amsterdam, April 12, 1994

Dear Dr. Umeki,

I am pleased to be able to inform you that the manuscript *Modelling the relationship between the asymmetry in crown display and local environment* by Umeki, K. has, in principle, been found acceptable for publication.

However, before it can be finally accepted for publication, I would like to ask if you could please send me a copy of the manuscript on floppy disk at your earliest convenience, as previously requested.

Upon receipt of the disk, the manuscript will be transferred to the copy editor for preparation for press.

I look forward to hearing from you.

Yours sincerely,
AGRICULTURAL SCIENCES SECTION

pp. Anthony McArdle
Mrs. N. de Jong

Umeki-1

A comparison of crown asymmetry
between a gymnosperm
and an angiosperm tree species

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1 Umeki, K. A comparison of crown asymmetry between a
2 gymnosperm and an angiosperm tree species.

3

4

5 Abstracts

6 Morphological plasticity in terms of asymmetric display
7 of crowns was compared between a gymnosperm tree species
8 (Picea abies Karst.) and an angiosperm tree species (Betula
9 maximowicziana Regel.). To evaluate crown asymmetry in
10 relation to local environment, a model that predicts crown
11 asymmetry from microtopography and configuration of
12 neighbors was applied to data derived from a mixed forest
13 in Hokkaido, northern Japan.

14 B. maximowicziana had greater crown asymmetry than P.
15 abies in absolute value. However observed crown asymmetry
16 of both species was determined by local environment to
17 similar degrees.

18 Some other differences were found between two species.
19 Crowns of P. abies were more influenced by neighbors than
20 microtopography, while crowns of B. maximowicziana more by
21 microtopography than neighbors. Crowns of P. abies were
22 influenced mainly by larger neighbors, while crowns of B.
23 maximowicziana also by relatively small neighbors. Crowns
24 of P. abies were influenced only by close neighbors, while
25 crowns of B. maximowicziana also by relatively far
26 neighbors to some extent.

1 Introduction

2 Trees intercept light by their crowns so that size and
3 shape of crowns play an important role in determining
4 growth of individuals and light regime in communities (e.g.
5 Kuuluvainen and Pukkala 1989; Hix and Lorimer 1990).
6 Plasticity in crown shape is also important because, with
7 this plasticity, trees can adjust their crowns to the
8 heterogeneity in light availability and intercept light
9 more efficiently (Kohyama 1980; Fisher and Hibbs 1982;
10 Shukla and Ramakrishnan 1986).

11 The morphological plasticity in resource-capturing organs
12 affects not only an individual's performance but also
13 phenomena at the population and community levels. For
14 example, crown asymmetry can modify the size distribution
15 of a population through changes in the growth of
16 individuals (Sorrensen-Cothorn et al. 1993), and spatial
17 structure in community (Ishizuka 1984). With asymmetric
18 root distribution, two plants can be close to each other
19 without competing (Brisson and Reynolds 1994). Crown
20 asymmetry also can affect gap dynamics because the
21 unbalanced crown distribution reduces the mechanical
22 stability of trees (Young and Hubbell 1991).

23 Morphological plasticity of modular organisms such as
24 trees is compared to behavior of unitary organisms (Waller
25 1986; Schmid 1992), and has been considered as a part of
26 species-specific strategies selected under a given
27 environment (Grime 1979; Chapin 1980). For example, Grime
28 (1979) divided species into several groups according to his
29 strategies which involve the degree of morphological

1 plasticity; competitors are more plastic than stress-
2 tolerators. Waller (1986) also supposed that gymnosperm
3 species, with their single trunk, strict whorls of
4 horizontal branches, and overall conical shape, are less
5 plastic than angiosperm species. He pointed out that less
6 plastic crown shape of gymnosperms may be related to their
7 habitat: marginal area with fewer competitors or recently
8 burned areas with uniformly high light intensities.

9 Although the discussions of adaptive linkage between
10 morphological plasticity and habitat should be based on
11 quantitative understanding of morphological plasticity,
12 data are rather scarce for tree species (Canham 1988). In
13 this paper, I evaluate the crown plasticity of a gymnosperm
14 tree (*Picea abies* Karst.) and an angiosperm tree (*Betula*
15 *maximowicziana* Regel.), and test Waller's supposition that
16 gymnosperms are less plastic than angiosperms.

17 I focus on one aspect of crown plasticity: the degree to
18 which crowns deviate from the stem base position (crown
19 asymmetry). If light environment is homogeneous around a
20 tree, the tree is expected to have a symmetric crown around
21 its stem. Therefore we can consider that observed crown
22 asymmetry develops through plastic response to
23 heterogeneity in light environment or accidental physical
24 factors in some cases. To quantify crown asymmetry, I use
25 crown-vector which links the stem base position of a focal
26 tree and the centroid of its projected crown area
27 (Takiguchi 1983; Umeki 1994), and employ a model that
28 predicts the crown-vector from local environment:
29 microtopography and neighbors (Umeki 1994). The following

1 questions are addressed: 1) How different are P. abies and
2 B. maximowicziana in the absolute magnitude of crown-
3 vector? 2) To what extent is the variation in observed
4 crown-vectors accounted for by local environment for the
5 two species? 3) Are there any differences between the two
6 species in the relationship between crown-vector and local
7 environment? On the basis of the results of the model
8 applications, species-specific characteristics in crown
9 plasticity are discussed in relation to basic crown shape
10 and regeneration habit of angiosperms and gymnosperms.

1 **Materials and Methods**

2 Data collection

3 The study site is located in a forest stand that
4 originated from a Picea abies plantation established in
5 1916. Hardwood species invaded just after Picea abies was
6 planted. Invasion of hardwood species made this stand a
7 mixed forest of hardwoods and conifers. The most dominant
8 hardwood species is Betula maximowicziana, and co-dominant
9 species is Magnolia obovata Thumb. Five 25 x 25 m² study
10 plots were set in the stand. All stems greater than 4cm in
11 diameter at breast height (dbh) were tagged and their dbh
12 and height were measured. Crown projection maps were
13 drawn. Trees were divided into two height classes: canopy
14 trees and understory trees. Here canopy trees are defined
15 as those whose crown is not overtoped at least in one part,
16 and understory trees as those whose crown is completely
17 overtoped by neighbors. All analyses in this paper were
18 restricted to canopy trees only. Microtopography in the
19 plots was measured with a survey compass. Details of
20 measuring protocol are given in Umeki (1994).

21

22 The Model

23 To quantify the crown asymmetry, I used crown-vector
24 which links stem base position and the centroid of
25 projected crown area (Fig. 1). It can express the
26 magnitude and direction of average deviation of crown
27 position from stem base (Umeki 1994).

28 To analyze the relationship between the crown asymmetry
29 and local environment, a model was applied in which crown-

1 vector of a focal tree is expressed by a function of its
 2 local environment (Umeki 1994). In the model, two factors
 3 (neighbors and microtopography) determine crown-vector; 1)
 4 trees avoid their neighbors, and 2) trees shift their crown
 5 toward the lower side of the slope. The model is given by:

$$6 \quad \mathbf{c} = H^l \left(a \sum_i \frac{h_i^m}{d_i^n} \mathbf{u}_i + b \boldsymbol{\alpha} \mathbf{v} \right)$$

8
 9 where $\mathbf{c}$ is the crown-vector; H is the height of a focal
 10 tree; h_i and d_i are the height of and distance to the i -th
 11 neighbor, respectively; $\mathbf{u}_i$ is the horizontal unit vector
 12 giving the direction from the stem base position of the i -
 13 th neighbor to that of the focal tree; $\mathbf{v}$ is the horizontal
 14 unit vector giving the direction of the steepest
 15 inclination of the slope; $\boldsymbol{\alpha}$ is the inclination of the slope
 16 on which the focal tree occurs; a , b , l , m , and n are model
 17 parameters to be fitted. The first term in the parenthesis
 18 expresses the effect of neighbors, and the second term the
 19 effect of microtopography; both terms are expressed by two-
 20 dimensional vectors. This model is divided into two
 21 elements when applied to data. We can standardize
 22 parameters a and b to express the relative strength of the
 23 effect of neighbors and microtopography, respectively (the
 24 standardized parameters are represented by a' and b').
 25 Parameter l indicates how the plastic response of a focal
 26 tree is dependent on its height. Parameter m indicates how
 27 the effect of neighbors is dependent on their height.
 28 Parameter n indicates how the effect of neighbors decreases
 29 with the distance from them.

1 To illustrate the effect of the parameters $\underline{l}$, $\underline{m}$ and $\underline{n}$,
2 crown-vectors were calculated in model populations of 15
3 individuals. Figure 2 shows crown-vectors in model
4 populations, in which only the neighbor effect act on each
5 tree as the influence of its environment (*i.e.* $b=0$).
6 Arrows in the diagrams show crown-vectors whose point and
7 base indicate the centroid of projected crown area and stem
8 base, respectively. The diameter of a circle around the
9 point of crown-vector is proportional to tree height. The
10 stem base position and tree height are identical for all
11 plots. The parameter $\underline{a}$ is so adjusted that all the
12 populations are equivalent in the mean magnitude of crown-
13 vectors. I set $\underline{l}=1$, $\underline{m}=1$, $\underline{n}=1$ as the base-line combination
14 of parameters (Fig. 2d), and varied one parameter in turn.
15 As the parameter $\underline{l}$, $\underline{m}$, or $\underline{n}$ increases or decreases, crown-
16 vectors change in direction and magnitude. When $\underline{l}$ is
17 positive, tall trees can have larger crown-vectors (Fig.
18 2a) while short trees can have larger crown-vectors when $\underline{l}$
19 is negative (Fig. 2g). When $\underline{m}$ is positive, the trees that
20 have tall neighbors have larger crown-vectors than those
21 that have short neighbors (Fig. 2b) while the trees that
22 have short neighbors have larger crown-vectors when $\underline{m}$ is
23 negative (Fig. 2f). When $\underline{n}$ is large, neighbors in close
24 vicinity of a focal tree alone exert visible effect on the
25 focal tree and the effect of far neighbors from the focal
26 tree is negligible (Fig. 2e). Meanwhile, the effect of
27 distant neighbors is also considerable when $\underline{n}$ is small
28 (Fig. 2c d).
29

1 Model Application

2 Canopy trees of B. maximowicziana and P. abies within 15
3 x 15 m² square in the center of each plot were used as
4 focal trees. Trees outside the center square were used
5 only as neighbors to minimize the edge effect. Data from
6 five plots were pooled. The model was applied to these
7 species separately.

8 If the parameter l, m, and n are given, the model can be
9 fitted by the multiple regression method without the
10 intercept. I tried various integer combinations
11 systematically on a computer, searching for the best-fit
12 values for l, m, and n, with which the coefficient of
13 determination was maximum. For statistical tests of
14 coefficient of determination (r^2) and standardized
15 parameters a' and b', I used Fisher's randomization method
16 with 5000 replications. Closer explanations of the model,
17 its calibration, and the statistical tests were given in
18 the previous paper (Umeki 1994).

1 Results

2 Although P. abies was greater than B. maximowicziana in
3 dbh and tree height, crown-vectors of B. maximowicziana
4 were much longer than those of P. abies (Table 1). This
5 means that crown shape of B. maximowicziana is more plastic
6 than that of P. abies in absolute value.

7 The coefficients of determination and estimated
8 parameters of the model are tabulated in Table 2. The
9 coefficients of determination for both species were high,
10 indicating crown asymmetry of both species was determined
11 by local environment to similarly high extent.

12 Both neighbors and microtopography had significant effect
13 on the crown shape for both species. However, the relative
14 strength of neighbors and microtopography were different
15 for the two species; crown shape of P. abies was more
16 influenced by neighbors, while that of B. maximowicziana
17 was more influenced by microtopography.

18 The estimated value for $\underline{l}$ was zero for both species,
19 indicating that the response of focal trees to their local
20 environment was not dependent on their height. Parameter
21 $\underline{m}$ was one for B. maximowicziana, while six for P. abies,
22 indicating that the influence of neighbors is linearly
23 dependent on their height for B. maximowicziana, and
24 disproportionately dependent on height for P. abies.
25 Parameter $\underline{n}$ was larger for P. abies than for B.
26 maximowicziana, indicating that crowns of P. abies were
27 influenced by neighbors within close vicinity only, whereas
28 crowns of B. maximowicziana were influenced also by
29 relatively far neighbors.

1 Discussion

2 The absolute magnitude of crown asymmetry of B.
3 maximowicziana expressed by the length of crown-vector was
4 larger than that of P. abies. However, it does not mean
5 that P. abies does not adjust its crown to heterogeneity in
6 local environment because the fit of the model for P. abies
7 was high. Thus Waller's supposition, that gymnosperm trees
8 are less plastic in their morphology holds as long as it
9 says about the absolute values. If his statement means
10 that gymnosperm trees do not respond plastically to their
11 environment, it is not true at least for this species.

12 The relationship between crown-vectors and local
13 environment can be summarized by the estimated model
14 parameters, some of which showed interesting differences
15 between these species.

16 Crowns of B. maximowicziana were more influenced by
17 microtopography than neighbors ($a' < b'$). On the other hand,
18 crowns of P. abies were determined more by neighbors than
19 microtopography ($a' > b'$). This contrast may be related to
20 the difference of basic crown shape of these species.
21 Microtopography determines the large-scale heterogeneity in
22 light availability because canopy is lower in the downward
23 direction of the slope than in the upward direction if the
24 canopy is parallel to the ground. Neighbors determine the
25 small-scale heterogeneity in light availability. Because
26 crowns of B. maximowicziana are wide, they are more likely
27 to be influenced by large-scale light heterogeneity
28 determined by microtopography. On the other hand, crowns
29 of P. abies are narrow so that they are more influenced by

1 the location of neighbors, which determines small-scale
2 heterogeneity in light.

3 The estimated values for λ were zero for both species.
4 Zero value for λ means that the response of focal trees is
5 independent of tree height. This is partly because of the
6 small range of height of analysed canopy trees.

7 Parameter μ was larger for *P. abies* than for *B.*
8 *maximowicziana*. This means that the effect of large
9 neighbors was disproportionately large for *P. abies* while
10 the effect of neighbors was linearly dependent on tree
11 height for *B. maximowicziana*, though the reason was not
12 clear.

13 Crowns of *P. abies* respond to only close neighbors to
14 them (μ was larger). It seems reasonable if we consider
15 the narrow crowns of this species because narrow crowns can
16 be influenced only by neighbors within relatively narrow
17 area around them. On the other hand, *B. maximowicziana* has
18 wide crowns. This is correspondent with smaller μ for this
19 species.

20 With these estimated parameters, we can evaluate the
21 species-specific characteristics in morphological
22 plasticity, which are important for individual trees to
23 occupy space in heterogeneous environment. In general,
24 hardwood trees can have large crown asymmetry. With this
25 ability, hardwood canopy trees can expand their branches
26 toward nearby gaps in the forest canopy, and saplings can
27 grow into a gap not only from just below the gap but also
28 from its peripheral area. On the other hand, many
29 gymnosperm trees are less capable of such opportunism; they

1 cannot have large crown asymmetry. Nevertheless, they can
2 adjust their crown shape to small-scale heterogeneity in
3 light availability avoiding their neighbors. It may have
4 relation with the regeneration habit of gymnosperm trees.
5 Gymnosperms often regenerate simultaneously in large open
6 area with uniformly high light; such stands contain
7 relatively few gaps (Waller 1986, Ishikawa and Ito 1989).
8 In this case, the ability of gymnosperms to avoid neighbors
9 close to one another is an effective strategy.

1 **Acknowledgment**

2 I thank Dr S. Watanabe and members of the Tokyo
3 University Forest in Hokkaido for their help in setting the
4 study plots and collecting data and Dr K. Kikuzawa for
5 several helpful suggestions on the manuscript.

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25 treefalls, and repeat disturbance of broad-leaved
26 forest gaps. *Ecology* 72: 1464-1471.

1 **Figure Legends**

2

3 Fig. 1. Schematic diagram of crown-vector. Crown-vector
4 is a horizontal vector which links stem base position and
5 the centroid of projected crown area.

6

7

8

9 Fig. 2. Effect of the parameters $\underline{l}$, $\underline{m}$, and $\underline{n}$ on crown-
10 vectors in model populations of fifteen individuals. The
11 stem base distribution and tree height are indentical for
12 all populations. Arrows are the crown-vectors. The
13 diameter of circles represent individual size (tree
14 height). The parameters $\underline{a}$ is so adjusted that nine
15 populations are equivalent in their mean length of crown-
16 vector. As the parameters $\underline{l}$, $\underline{m}$ or $\underline{n}$ increases or decreases
17 from the base-line combination ($\underline{l}=1$, $\underline{m}=1$, $\underline{n}=1$), the crown-
18 vectors vary in their direction and magnitude. See text
19 for details.

Table 1. DBH, tree height, and the length of crown-vector of Betula maximowicziana and Picea abies. Significances of the difference between two species are tested by Man-Whitney U test.

Species	DBH	Height	Crown-Vector Length
<u>B. maximowicziana</u>	24.0 (1.2)	21.0 (0.8)	4.4 (0.3)
<u>P. abies</u>	31.4 (1.2)	25.5 (0.8)	0.6 (0.1)
difference	<0.01%	<0.01%	<0.01%

Table 2. Coefficients of determination and estimated parameters of the model. *** and * show that the coefficient or the parameter is significant at the 0.1% and 5% level, respectively, by Fisher's method of randomization.

Species	No.	r^2	a''	b'	l	m	n
<u>P. abies</u>	22	0.65***	0.66***	0.37***	0	6	2
<u>B. maximowicziana</u>	22	0.76***	0.27*	0.78***	0	1	1

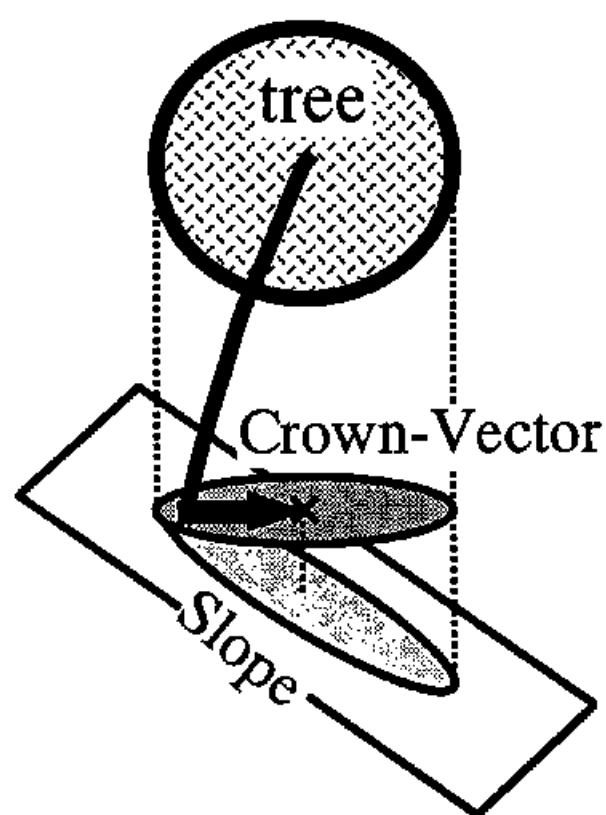


Fig. 1

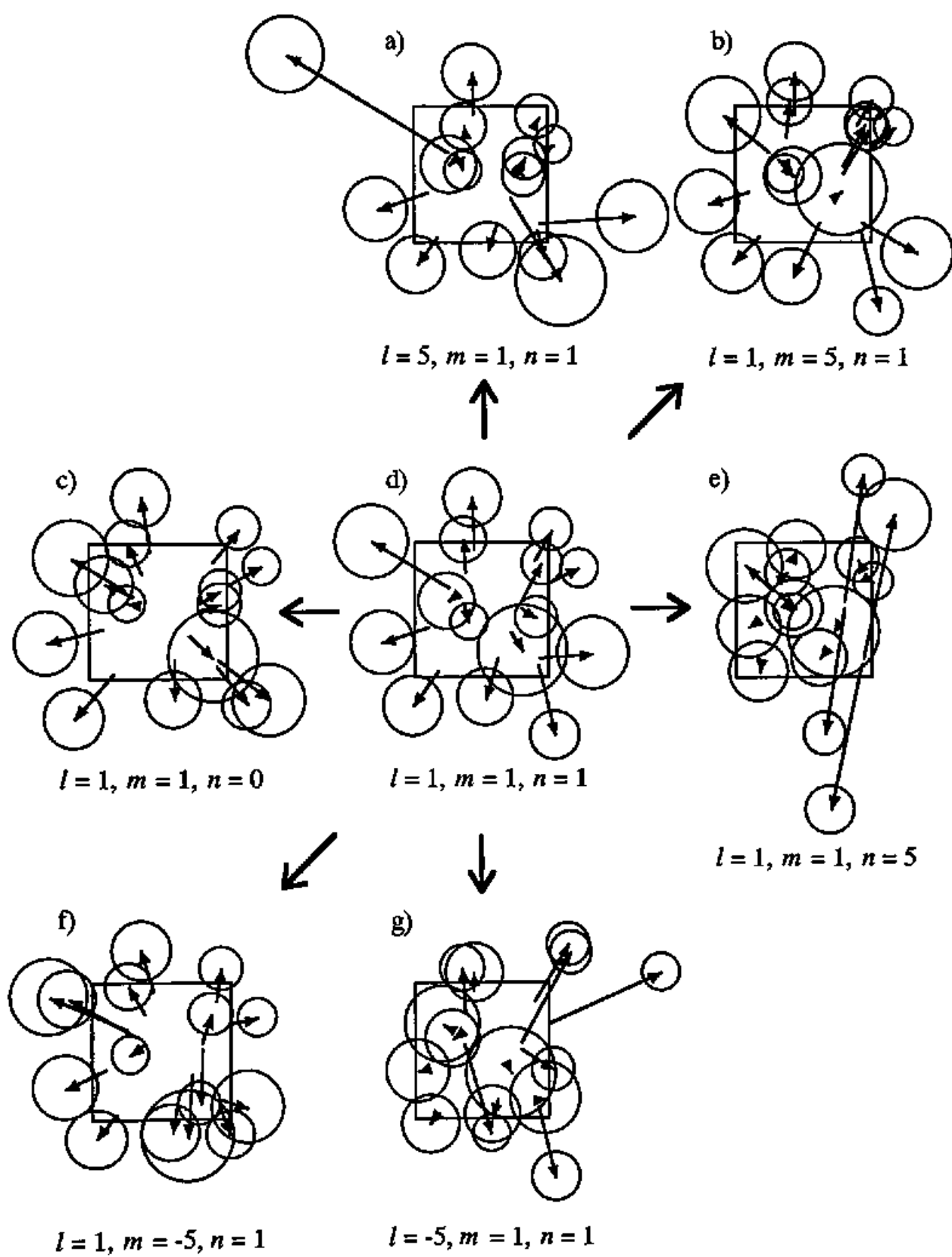


Fig. 2

Importance of crown position and
morphological plasticity in
competitive interaction in a
Population of Xanthium canadense.

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Running Title

Competition and morphological
plasticity in Xanthium Population

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ABSTRACT

Interactions between individuals in terms of asymmetric display of crowns and reduction of growth were followed in an experimental population of Xanthium canadense.

Competitive interaction was analyzed using a neighbourhood interference model. For the analysis of morphological interaction, Crown-vector, which was a two-dimensional vector that joined the stem base position of a plant with the centroid of its projected crown area, was used to express the direction and magnitude of the asymmetry in crown display. A model was developed in which the change in crown-vector during a growth period was expressed as a function of both the size of the focal plant and the size and location of its neighbours.

There was strong morphological interaction between crowns; they repelled each other. The competitive interaction was detectable by the competition model with crown-centers used as plant locations, but not detectable with stem bases used as plant locations.

It was concluded that the positions of neighbours' crowns were important in determining the growth and crown asymmetry which in turn determine the crown location, and morphological plasticity in crown shape works to reduce interference between individuals.

KEYWORDS

Crown asymmetry, Xanthium canadense, cocklebur,
neighbourhood effect, morphological plasticity

INTRODUCTION

Individual plants growing in a population interact with their neighbours in many ways (Harper, 1977). Competitive interactions, in which the growth of an individual plant is reduced by the presence of neighbours, have been studied extensively (for example, Grace and Tilman, 1990). On the other hand, the presence of neighbours affects plant morphology (for example, Solangaarachchi and Harper, 1989). This morphological plasticity can in turn modify the competitive interaction, due to changes in the distribution of resources as resource-capturing organs such as foliage or roots develop plastically (Sorrensen-Cothorn, Ford, and Sprugel, 1993). Thus, we need understand both competitive and morphological interactions in populations.

Let us consider one morphological type of plant species: those having a vertical main stem and potentially symmetric branch systems around the stem. I focus on one aspect of morphology of such plants: the degree to which the crown is symmetrically centered on the stem base. If the light environment around a plant is horizontally heterogeneous, the plant has an asymmetric crown, due to differential growth of module populations in the crown (Jones and Harper, 1987a, b; Franco, 1986; Solangaarachchi and Harper, 1989; Novoplansky, Cohen, and Sachs, 1990) because module populations grow vigorously in sun-lit regions of the crown, and slowly in shaded regions. This asymmetry in crown display modifies the local light condition in the population, which may influence the development of crowns.

Crown asymmetry can be considered adaptive, because plants can place their foliage in the favorable space where they can intercept more light. Such asymmetry is useful in studying morphological plasticity. When a plant occurs in an ideal condition where environment is homogenous around the plant, it is expected to have a symmetric crown around its stem, that is, asymmetry in crown display is zero. This means that the control, with which observed values must be compared, is always zero. Thus we can consider that the observed asymmetry is the result of heterogeneity of environment so that we can correlate observed asymmetry with heterogeneity of environment directly.

There are two types of spatial models that can deal with competitive and/or morphological interaction: one describes a plant as a population of subunits, the other assumes a plant as a point that has some traits such as size. Some growth models have been proposed that assume a plant as a population of subunits (Bell, 1984; Ford, 1987; Koike, 1989; Sorrensen-Cothorn et al., 1993). In these models, the size and morphology of an individual plant can be expressed by the number and the distribution of subunits in space. Because they involve the information at the lower level than individual (the number and angle of branches, foliage density distribution, or growth of sector of whorl) together with information at the individual level, estimation of parameters and calibration of their model in the field are difficult. While many competition models in which a plant is represented by a point have been proposed (Mack and Harper, 1977; Ford and Diggle, 1981; Weiner, 1982, 1984;

Pacala and Silander, 1985; Biging and Dobbertin, 1992; Judson, 1994), those addressing the morphological interaction at the individual level are rare (Umeki, 1994). Umeki (1994) proposed a simple model that describes the morphological interaction at the individual level. However, it was a static model in which the crown asymmetry of a plant at a given time is related to its local environment at that time. Models that can predict the dynamic morphological process at the individual level are necessary in order to build model systems, which incorporate sub-models for competitive and morphological interactions. Such model systems would enable us to analyze both interactions at the individual level, and to understand how they work in a given population. Although stem base position has been used as the representing point of a plant in many models, whether it is appropriate has not been addressed.

In this paper, (1) growth and the change in crown asymmetry of individuals are followed in an experimental population. (2) A dynamic model is proposed in which the development of the crown asymmetry is expressed as a function of both the size of a focal plant and the size and position of its neighbours. (3) The morphological and competitive interactions are analyzed using the newly proposed model for crown asymmetry and the neighbourhood interference model, respectively.

I address the following questions: (1) Which is more appropriate representative position of individual plants, stem base position or crown-center? (2) How does the change in crown asymmetry is related to the size of focal plant and

its neighbours and the distance from neighbours? (3) How does competitive status change due to crown asymmetry?

MATERIALS AND METHODS

Data Collection

Xanthium canadense Mill. is a large annual plant (up to 2.5 m high) whose above-ground architecture is characterized by one vertical main stem and many long lateral branches. It can develop a horizontally asymmetric crown by modifying the number and length of first-ordered branches. Twenty-five seedlings of X. canadense were collected in a nursery of Kyoto University, Kyoto city, central Japan, and transplanted randomly in a 5x10 m² plot in the same nursery in the middle of May in 1989. The planting density was 0.5 plant per square meter.

I measured plant height (h) and stem diameter at the ground level (d) from 31 May to 6 September, at intervals of approximately one month. Above-ground dry mass (S) was estimated using the function $S=ah^bd^c$ (where a , b and c are constants), which was fit using a multiple linear regression of log-transformed variables obtained from harvested sample plants. These sample plants were grown under the same conditions in the nursery some distance apart from the plot. The prediction equation explained 98% (n=32) of the variance in log above-ground dry mass.

I drew crown projection map at each census. I drew the outlines of the projected shapes of crowns on the ground with the help of an iron stick which indicated points on the ground just below the edge of crowns. The projected crowns on the ground were, then, drawn on a section paper with the

help of grids of 50 cm intervals on the ground. The last census (6 September) was just after the onset of flowers.

Expression of the Crown Asymmetry

In this paper, I use the crown-vector, which is a two-dimensional vector that joins the stem base position of a plant with the centroid of its projected crown area, to express the direction and magnitude of the crown asymmetry (Takiguchi, 1983; Umeki, 1994). The centroid of each projected crown (Hereafter crown-center) was determined by cutting paper outlines of projected crown and suspending each from multiple pivot points.

The models

For the analysis of the change in crown-vectors, a new model was developed. It expresses the tendency of proximal crowns to repel each other. It is formulated by a difference equation expressed by vectors, in which the change in the crown-vector from time t to $t+1$ is expressed as the product of the influence (G_t : vector) of the neighbours at time t and the response (F_t : scalar) of the focal plant to the influence. Thus it is expressed as:

$$\Delta C_t = C_{t+1} - C_t = F_t G_t + e, \quad (1)$$

where C_t and e denote the crown-vector and an error vector, respectively.

The influence of a neighbour upon a focal plant is assumed to have the magnitude proportional to the m -th power of the height of the neighbour and inversely proportional to the n -

th power of the distance between the focal plant and the neighbour, and to have the direction from the neighbour to the focal plant. The effects of different neighbours are summed as:

$$G_t = \sum_i \frac{h_{i,t}^m}{d_{i,t}^n} u_{i,t} , \quad (2)$$

where $h_{i,t}$ denotes the height of the i -th neighbour at time t ; $d_{i,t}$ is the distance between the i -th neighbour and the focal plant; $u_{i,t}$ is the horizontal unit vector giving the direction from the i -th neighbour to the focal plant.

The response of a focal plant is assumed to depend on its height, expressed as:

$$F = aH_t^l , \quad (3)$$

where H_t denotes the height of the focal plant at time t ; a and l are model parameters.

Equations 2 and 3 are substituted into eqn 1 as:

$$\Delta C = aH_t^l \sum_i \frac{h_{i,t}^m}{d_{i,t}^n} u_{i,t} + e. \quad (4)$$

When calibrating this with data, eqn 4 is divided into two elements according to orthogonal coordinate axes x and y .

If parameters l , m , and n are given, the model can be calibrated and parameter a can be estimated by the ordinary regression method without intercept. I used the statistic $r^2 = 1 - \sum (x - \hat{x})^2 / \sum (x - \bar{x})^2$ (the coefficient of determination) to evaluate the fits of the model. Trying various combinations of values for parameters l , m , and n

systematically on a computer, I searched the best-fit combination of parameters with the precision of 0.1.

To analyze the competitive interaction, I employed an individual-based interference model which incorporates asymmetry in competition (Thomas and Weiner, 1989). In this model, an index indicating the interference of neighbours (W) was given to each individual. W is expressed mathematically as:

$$W = \sum_{i=1}^n \begin{cases} kS_i d_i^{-2}, & S_i \geq S_f \\ kS_i d_i^{-2}(1-A), & S_i < S_f \end{cases} \quad (5)$$

where S_i and S_f are the size of the i -th neighbour and the focal plant, respectively; d_i is the distance to the i -th neighbour; and n is the number of neighbours within some distance of the focal plant; A is an asymmetry coefficient which varies from zero (symmetric competition) to one (completely asymmetric competition), and represents the degree to which the effects of relatively smaller neighbours are discounted; k is a constant. I made regressions of relative growth rate in terms of above-ground dry mass against W with 11 values of A ranging from 0.0 to 1.0 and ten values of the radius of neighbourhood (a circle neighbours within which are involved into W) ranging from 100 cm to 1000. I included all individual in the regressions; the sample size of regressions was 25.

In both analyses mentioned above, the location of a plant must be represented by a point in the horizontal plane. I used two different points as the representative of a plant: stem base position and crown-center.

The above models were applied to data of three growth periods of approximately one month: growth period I (from 31 May to 4 July), II (from 4 July to 3 August), and III (from 3 August to 6 September).

Statistical Test

Since the predictor variables in the above models are not independent, the ordinary test of the fit of model cannot be used (Fowler, 1984; Mitchell-Olds, 1987; Thomas and Weiner, 1989). Fisher's Method of Randomization provides a distribution-free test of association when observations are not independent (Sokal and Rohlf, 1981). For testing the significance of the competitive interaction, null distributions of coefficient of determination were generated by randomly assigning observed plant size and RGR values to observed plant positions using 5000 permutations for each test. The null hypothesis for competitive interaction is that the change in plant size is not related to plants' spatial positions. For testing the significance of the morphological interaction, observed plant size and crown-vector values were randomly assigned to observed plant positions. The null hypothesis for morphological interaction is that the change in crown-vectors is not related to plants' spatial positions.

Spatial Pattern

I employed Hopkins' test (Diggle, 1983) to quantify spatial pattern. The index for Hopkins' test is given by

$$H = \frac{\sum x_i^2}{\sum y_i^2},$$

where H is the index for Hopkins' test, x_i denotes the distance from i -th random point in the population to the nearest neighbour (plant), and y_i the distance from i -th randomly sampled plant to the nearest neighbour. Summations are over $i=1, \dots, m$, where m is the number of sampling points (random points or randomly sampled plants). I adopted 60 as m . When H is greater than one, individuals are aggregated, and regular when it is less than one. For a random spatial pattern, H has an F distribution with $(2m, 2m)$ degree of freedom so that we can test whether a given spatial pattern departs from randomness toward clustering or regularity using H . I calculated H from the locations of stem bases and those of crown-centers at each census.

RESULTS

Growth

No individuals of the studied population died. At the end of the experiment, the average ($\pm$ SD) height and above-ground dry mass was 194 ± 20 cm and 1009 ± 291 g, respectively, and the average ($\pm$ SD) length of crown-vector was 43 ± 26 cm. All crowns kept touching with the ground at the lowest part since the second measurement (4 July).

Morphological Interaction

The fits of the model for crown-vector were highly significant throughout the experiment, and increased with time (Fig. 1a). They were better when $\bar{W}$ was calculated with location measured by crown-center than when $\bar{W}$ was calculated with location measured by stem base. The model parameter $\bar{I}$ did not change consistently; it was stable around unity with location measured by crown-center (Fig. 1b). Parameters $\bar{m}$ and $\bar{n}$ decreased consistently with time (Fig. 1c d).

Spatial Pattern

The index for Hopkins' test (H) for stem base positions did not differ from one, indicating that their spatial pattern was random (Table 1). On 31 May spatial pattern of crown-centers did not differ from random because crown-vectors were too small to make their spatial pattern different from that of stem bases. As population grew, the index for Hopkins' test decreased, indicating that spatial patterns of crown-centers became regular. No two crown-

centers were closer than 71 cm on 3 August and 6 September, while the nearest distance between stem bases in the population was 28 cm.

Competitive Interaction

The index for neighbourhood interference ($\bar{N}$) did not account for the variance of RGR for any given growth period, when $\bar{N}$ was calculated with location measured by stem base (Table 2). When $\bar{N}$ was calculated with location measured by crown-center, it accounted for the variance of RGR for growth period II and III significantly (Table 2). The best-fit coefficient of asymmetry in competition ($\bar{A}$) was always zero, indicating that the competitive interaction was two-sided.

Effect of crown plasticity on competitive status

Neighbour interference must have been reduced by crown plasticity, because crowns repelled each other due to crown plasticity, and neighbour interference decreases with the distance. To evaluate the effect of crown plasticity on competitive status of individual plants, I calculated $\bar{N}$ using stem base as plant location with the best-fit neighbourhood radius and competitive asymmetry for the model with location measured by crown-center. It can express the neighbour interference experienced by individuals if they had no crown asymmetry (*i.e.* if they had their crowns just above stem bases). The indecis of interference ($\bar{N}$) calculated with stem base position as plant location were greater than $\bar{N}$ s calculated with crown-center especially for

later growth (Table 3) indicating that plants avoided strong interference due to crown asymmetry.

DISCUSSION

There was strong morphological interaction in the population analyzed. The model for crown-vector accounted for the change in crown-vector in all growth periods (Fig. 1a), indicating that the crowns of *X. canadense* grew away from their neighbours. This plastic response resulted in the regular spacing of crown-centers (Table 1). This result was consistent with the observation of Ishizuka (1984) that the spatial patterns of crown-centers were more regular than those of stem bases in forest communities.

Throughout the experiment, coefficients of determination were higher when crown-centers were regarded as the locations of plants than when the stem base positions were regarded as the locations of plants. This indicates that crown location is more important in the morphological interaction than that of stem base. This seems reasonable, when we consider that the interaction in this case might be mediated by local light condition, which are modified by proximal crowns.

The estimated model parameters λ , μ , and η show some of the interactions between neighbours and focal plants in this population. The parameter μ decreased with time, indicating that only larger plants exerted considerable effect on the crown display of their neighbours during early growth, while smaller ones also came to do so as the population grew. The model parameter η also decreased with time, indicating that the influence of neighbours decreased with distance less rapidly during later growth than earlier. One possible

explanation for these parameter changes is related to the change in individual sizes. Before an individual reaches a certain size, it cannot modify the light environment enough to affect its neighbours. Thus, during earlier growth, some individuals were smaller than the critical size, so that the parameter $\underline{m}$ was larger. Later, all plants were large enough to affect morphology of neighbours so that $\underline{m}$ was smaller. The zone within which an individual influences its neighbours is expected to become larger as the individual grows. This change is expressed by the decrease in the parameter $\underline{n}$ in this model, which therefore reflects the growth of this zone of influence. The model parameter $\underline{l}$ remained stable around unity with crown-centers used as plant location. This indicates that the ability of individuals to make their crown shapes asymmetric is almost proportional to their height.

The index of interference ($\underline{W}$) accounted for the variance in RGR when it was calculated with crown-center used as plant location, but did not with stem base used as plant location. This, again, indicates that crown location is more important in the competitive interaction than that of stem base. As in morphological interaction, this seems reasonable, when we consider that the interaction may be mediated by local light conditions, which are modified by proximal crowns. These results clearly show that crown-center is more appropriate representative position for an individual plant than stem base when interaction is mediated by light. Silander and Pacala (1985) also showed that the fit of their neighbourhood interference model increased when

the displaced positions of rosettes were substituted for the original plant positions, and pointed out that displacement of rosettes may be a mechanism by which small scale clumping is reduced as a result of local plant interference. It is likely that the fit of neighbourhood interference models increases if proper representation such as crown-center is substituted for stem base position.

It does not necessarily mean that the measure of interference calculated with stem base position used as plant location always fails to detect competitive interaction when competition is mediated by local light condition. They can account for the variance in plants' performance when stem bases are close to the corresponding crown-centers, that is, when crown plasticity is not so important that it does not change the relative position to neighbors. There are some cases in which the crown plasticity is not important for competitive interaction. First, when spatial pattern of stem bases is regular and plant sizes are similar, crown plasticity cannot change spatial pattern. It can occur when planting pattern is already regular (as in Cannell, Rothery, and Ford, 1984). It can also occur when density-dependent mortality makes spatial pattern regular (Kenkel, 1988; Moeur, 1993). Second, the ability of crowns to adjust their shape plastically depends on species and/or genotype (Waller, 1986; Solangaarachchi and Harper, 1989); change in crown spacing due to crown asymmetry may be less important for some species.

When interaction is mediated by under-ground resources (Weiner, 1982), the similar thing can be said; stem base may not be appropriate representative point for an individual plant, if the distribution of roots is not symmetric around stem base due to plastic development (Crick and Grime, 1987).

The best-fit index of competitive asymmetry (Δ) was always zero (Table 2), indicating that the competitive interaction was two-sided. It is not surprising even if the competitive interaction may be mediated by light, which often makes competition one-sided. The lowest part of all crowns touched the ground so that lower parts of crowns of larger plants were shaded by crowns of smaller plants. This can make competition two-sided even if competition is for light (Yokozawa and Hara, 1992).

Individual plants can avoid strong competition by this morphological plasticity (Table 3). Therefore this plasticity is important for an individual performance and also for population dynamics. In the X. canadense population analyzed, more strong interference would be expected and mean above-ground dry mass would be smaller, if plants did not have asymmetric crowns.

This modification of competitive interaction by crown asymmetry has some effects on phenomena at the population level. For example, crown plasticity can reduce the effect of spatial pattern of stem base on size structure of populations. Weiner (1985) expected that the size inequality in experimental populations of Trifolium incarnatum and Lolium multiflorum was greater when the

spatial pattern of stem bases was random than when it was regular, but found that the effect of spatial pattern on size variability was weak. He suggested that it might be because plastic growth of crowns greatly influenced the proximity of a plant to its neighbours, and spatial relationships.

Sorrensen-Cothorn et al. (1993) incorporated crown asymmetry in their competition model for conifers. They proposed that local shading at the branch level causes crown asymmetry, so that competitive branch interaction is the main cause for plastic morphology at the individual level. However, morphological interaction in X. canadense population began to work before crowns touched each other in the middle of July. Ballaré et al. (1988) also reported that Datura ferox seedlings responded morphologically to their neighbours before light intensity was reduced by the neighbours. The proximate mechanism of morphological plasticity of many plant species, including Xanthium, has been proved to involve light quality (Bogorad and McIlrath, 1960; Casal, Deregibus, and Sánchez, 1985; Deregibus et al., 1985; Ballaré et al., 1988; Ballaré, Scopel, and Sánchez, 1990; Novoplansky et al., 1990). In summary, competitive and morphological interactions differ in time of occurrence, strength, and the underlying mechanism. They should, therefore, be treated separately when modelled at least for these species. It is important to note, though, that the relative importance of photomorphogenesis depends upon species and/or genotype (Skálová and Krahulec, 1992; Schmitt and Wulff, 1993). For example, local shading at the branch

level also effects the development of conifer crown asymmetry (Sorrensen-Cothorn et al, 1993).

In the present paper, an individual-based model was proposed to describe the dynamic process of crown asymmetry. Although crown asymmetry is only one aspect of morphological plasticity, it plays an important role in the growth of individuals and the dynamics of a population by reducing the competitive interaction. The model proposed in this paper, together with the neighbourhood interference model, forms a model system with which we can describe and analyze the morphological and competitive interactions simultaneously in a population at the individual level.

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Figure Legends

Fig. 1. Coefficients of determination (r^2) and estimated parameters of the model for crown-vector. Circles and squares in each diagram indicate coefficients of determination and parameters obtained when stem base positions and crown-centers were considered as the locations of plants, respectively. Asterisks (***) indicates that the coefficient of determination is significant at 0.1% level.

Table 1. Spatial patterns of stem bases and crown centers. Spatial pattern of each configuration is expressed by the index for Hopkins' test for randomness (H). Asterisks (****) show that the spatial pattern differs from random at 0.01 % level by F test. See text for details.

Position of individual	Date	H
Stem Base		0.94
Crown-Center	31 May	0.89
	4 Jul	0.80
	3 Aug	0.56****
	6 Sep	0.45****

Table 2. Coefficients of Determination and best-fit parameters of the competition model with plant location measured by stem base and crown-center. The sample number of regressions is 25. Asterisk shows that the coefficient of determination is significant at 5 % level by Fisher's Method of Randomization.

Growth Period	Plant Location	Coefficient of Determination	Neighbourhood Radius	Competitive Asymmetry
I	Stem Base	0.04 ^{ns}	400	0.0
	Crown-Center	0.04 ^{ns}	400	0.0
II	Stem Base	0.09 ^{ns}	100	0.0
	Crown-Center	0.25 [*]	100	0.0
III	Stem Base	0.04 ^{ns}	500	0.0
	Crown-Center	0.23 [*]	200	0.0

Table 3. Means and standard deviations (n=25) of the measure of interference ($\bar{W}$). $\bar{W}$ s are calculated with crown-center and stem bases used as plant locations. For neighbourhood radius and competitive asymmetry (Δ), the best-fit values for the competition model with crown-centers used as plant locations are used. Asterisks (****) show that $\bar{W}$ in terms of crown center and stem base are different at 0.01 % level by Wilcoxon signed rank test. See text for details.

Growth Period	$\bar{W}$ (Crown-Center)	$\bar{W}$ (Stem Base)	Difference
I	0.002 (0.002)	0.027 (0.019)	****
II	0.019 (0.022)	0.349 (0.255)	****
III	0.192 (0.116)	4.858 (3.514)	****

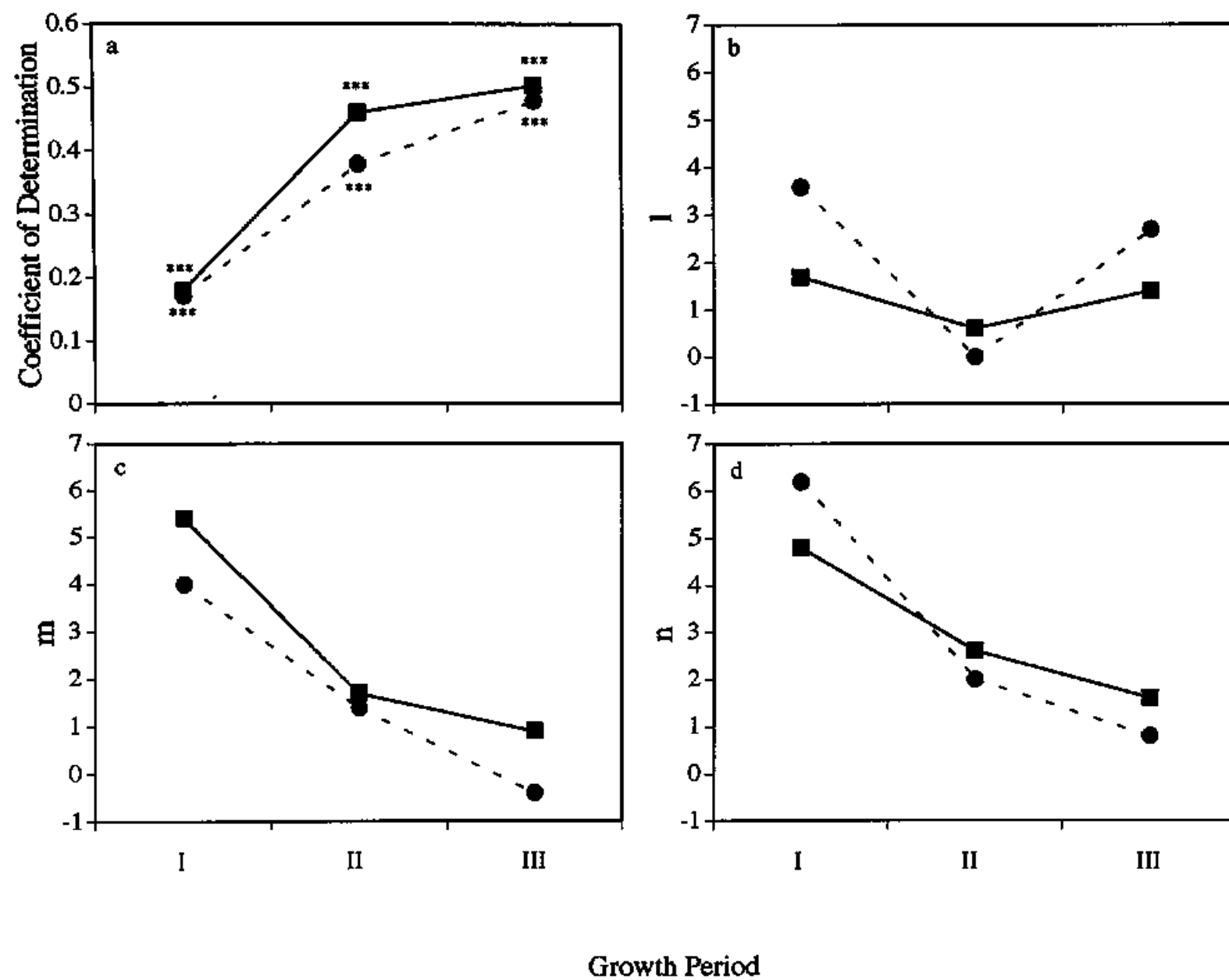


Fig. 1

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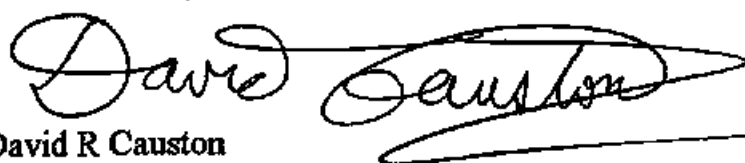
MS 94/84 '

Dear Dr Umeki

Many thanks for your letter in answer to my two small queries. I now have pleasure in accepting your paper for publication in the *Annals of Botany*. I have made a number of minor editorial changes to improve the English, but I must say that you write excellent English, and the paper reads well.

Thank you for submitting the results of this interesting work to the *Annals of Botany*.

Yours sincerely



David R Causton