

REVIEW

## Development of the Monsi–Saeki Theory on Canopy Structure and Function

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- *Background and Aims* Monsi and Saeki (1953) published the first mathematical model of canopy photosynthesis that was based on the light attenuation within a canopy and a light response of leaf photosynthesis. This paper reviews the evolution and development of their theory.
- *Scope* Monsi and Saeki showed that under full light conditions, canopy photosynthesis is maximized at a high leaf area index (LAI, total leaf area per unit ground area) with vertically inclined leaves, while under low light conditions, it is at a low LAI with horizontal leaves. They suggested that actual plants develop a stand structure to maximize canopy photosynthesis. Combination of the Monsi–Saeki model with the cost–benefit hypothesis in resource use led to a new canopy photosynthesis model, where leaf nitrogen distribution and associated photosynthetic capacity were taken into account. The gradient of leaf nitrogen in a canopy was shown to be a direct response to the gradient of light. This response enables plants to use light and nitrogen efficiently, two resources whose supply is limited in the natural environment.
- *Conclusion* The canopy photosynthesis model stimulated studies to scale-up from chloroplast biochemistry to canopy carbon gain and to analyse the resource-use strategy of species and individuals growing at different light and nitrogen availabilities. Canopy photosynthesis models are useful to analyse the size structure of populations in plant communities and to predict the structure and function of future terrestrial ecosystems. © 2004 Annals of Botany Company

**Key words:** Monsi–Saeki theory, Boysen Jensen, canopy photosynthesis, light, nitrogen, resource use, cost–benefit analysis, competition, coexistence, size structure, model, plant community.

### INTRODUCTION

Masami Monsi (1914–1997) and Toshiro Saeki (1927–2004) published the paper ‘Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion’ (‘On the factor light in plant communities and its importance for matter production’) in the *Japanese Journal of Botany* in 1953. This paper is now well known as the first that presented a mathematical model of canopy photosynthesis. They quantified attenuation of light through the canopy and modelled canopy photosynthesis as an integration of photosynthesis of leaves exposed to different light climates in the canopy. They demonstrated that stand structures develop to maximise canopy photosynthesis under a given light climate. The paper opened a new research area on canopy structure and function and is still an inspiration for plant ecologists, botanists and agronomists today. Yet, in spite of its importance, its acceptance by scientists in the western hemisphere was delayed by more than ten years (de Wit, 1965; Monteith, 1965; Ross, 1981; for review see Monsi *et al.*, 1973), probably because it was published in German in a local journal.

There is a history behind the development of any new idea, and the Monsi–Saeki theory is no exception. It has its roots in the work of Boysen Jensen (1932), a Danish plant physiologist. Boysen Jensen (1883–1959) was the founder of the science of dry mass production of plants. He wrote in the preface of his book (1932) that ‘sie bilden einen Versuch, den Schwerpunkt der Lehre von der Stoffproduktion der Pflanzen dorthin zu verlegen, wo sie meiner Meinung nach liegen muß: In die CO<sub>2</sub>-Assimilation der Blätter’

(‘those publications attempt to shift the emphasis of the study of biomass production by plants to where, according to me, it should be: leaf CO<sub>2</sub> assimilation’). He thus emphasized CO<sub>2</sub> assimilation of leaves in the study of dry mass production in plants. He first studied canopy photosynthesis in relation to stand structure, and suggested the importance of leaf arrangement in the plant stand. Suppose a stand has a LAI (leaf area index, total leaf area per unit ground area) of 3, i.e. the stand maintains a leaf area three times more than the ground area beneath it. When leaves are arranged horizontally as shown in Fig. 1A(a), only leaves in the first layer receive full light, whereas leaves in lower layers receive light that has penetrated the first layer and that is close to or less than the light compensation point. If the same amount of leaf area is arranged with inclinations within the canopy [Fig. 1A(b)], then light reaches every leaf more uniformly. Boysen Jensen noted that actual plants indeed have canopies with vertically inclined rather than horizontal leaves to distribute light uniformly within the canopy and thus to use light efficiently. For another example, Boysen Jensen established a small experimental stand of plants to measure the whole-canopy photosynthesis of the stand. He demonstrated that canopy photosynthesis was not saturated, while photosynthesis of a single leaf was saturated at relatively low light intensities (Fig. 1B).

### THE MONSI–SAEKI THEORY OF CANOPY PHOTOSYNTHESIS

Monsi and Saeki (1953) refined the idea of Boysen Jensen to develop a quantitative theory of canopy structure and function. They devised a stratified clipping technique to describe

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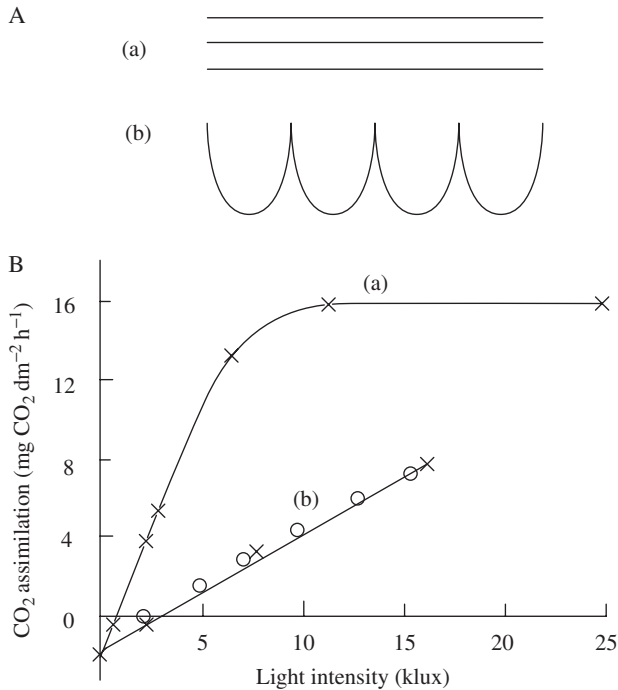


FIG. 1. (A) Schematic arrangements of photosynthetic tissues. (a) Three layers of photosynthetic tissues placed horizontally. (b) The same area placed with inclination. (B) Light-response curve of photosynthesis of (a) a single leaf and (b) a stand of *Sinapis alba*, where both are presented on a leaf area basis. Stand photosynthesis is obtained by multiplying  $b$  by 3.4 (= LAI). Canopy photosynthesis calculated with eqn (4) by Monsi and Saeki (1953) is added as open circles. Redrawn with modifications from Boysen Jensen (1932). Note that 1 klux corresponds to  $18 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  for daylight PAR (Larcher, 1995).

the structure of plant communities. Vertical distribution of plant mass was presented in a figure separately for photosynthetic and non-photosynthetic tissues together with a distribution of light intensity (see fig. 1 in Monsi and Saeki, 1953; reproduced in this issue). This figure was named 'the productive structure of a plant community' to imply that plant function is determined by the structure of the stand and, inversely, that the stand structure is determined by plant functions. Light attenuates more strongly in a stand of plants having horizontal leaves (broad-leaf type) than in a stand with vertical leaves (grass type). They found that light attenuation in the canopy was approximated by Beer's Law:

$$I = I_0 e^{-KF} \quad (1)$$

where  $I$  is the photosynthetic photon flux density (PPFD) measured on a horizontal plane,  $F$  is the leaf area index cumulated from top of the canopy, and  $K$  is the extinction coefficient.  $I_0$  is the PPFD above the canopy. They showed that if small horizontal leaves were distributed randomly in the canopy,  $K$  should be equal to 1. In reality, leaves are not small enough to comply with theory and are sometimes large, they are not horizontal but inclined, and they are not randomly distributed but are clumped or uniformly distributed.  $K$ -values deviate from 1 accordingly, and change from 0.3 to 2.0 (Monsi and Saeki, 1953). They noted that  $K$

in a canopy with horizontal leaves was commonly 0.7–1.0, whereas  $K$  in a canopy with vertically inclined leaves was 0.3–0.5.

The PPFD that leaves receive within the canopy ( $I'$ ) is different from PPFD on a horizontal plane ( $I$ ) because leaves are not horizontally distributed in the canopy. They showed that  $I'$  is calculated from eqn (1) as

$$I' = \frac{I_0 K e^{-KF}}{1-m} \quad (2)$$

where  $m$  is the transmittance of a leaf (Saeki, 1960). It is assumed that only leaves intercept PPFD in the canopy. A rectangular hyperbola was employed to describe the net photosynthesis of a single leaf ( $p$ ) as a function of  $I'$ :

$$p = \frac{bI'}{1+aI'} - r \quad (3)$$

where  $a$  and  $b$  are constants that characterise the light-response curve, and  $r$  is dark respiration (Tamiya, 1951). Substituting eqn (2) into (3) and integrating with respect to  $F$  from 0 to  $F$ , they calculated canopy photosynthesis,  $P$ , as

$$P = \frac{b}{ak} \ln \frac{(1-m) + aKI_0}{(1-m) + aKI_0 e^{-KF}} - rF \quad (4)$$

(Monsi and Saeki, 1953; Saeki, 1960). This equation was tested with the *Sinapis alba* stand of Boysen Jensen assuming  $m = 0$  and  $K = 1$ , and with the parameters for leaf photosynthesis of this species (Fig. 1B). The result (table 8a in Monsi and Saeki, 1953) gave a good agreement with the experimental result, as is shown by the open circles here in Fig. 1B. Equation 4 implies that canopy photosynthesis is determined by stand structure ( $K$  and  $F$ ), leaf physiology ( $a$ ,  $b$  and  $r$ ), an optical property of a leaf ( $m$ ), and the light environment ( $I_0$ ).

Figure 2A shows canopy photosynthesis under full light conditions as a function of  $F$ . Canopy photosynthesis of the stand is maximized with a low  $K$  at a higher  $F$ . This result demonstrates well why many canopies developing under full sunlight have a value of  $K$  around 0.7 and LAI around 5. The optimal LAI is defined by the lowest leaves that receive PPFD at the light compensation point ( $I'_c$ ), where daily leaf photosynthesis is cancelled out by respiration. At the light compensation point, the following two equations hold:

$$I'_c = \frac{I_0 K e^{-KF}}{1-m} \quad (5)$$

and

$$\frac{bI'_c}{1+aI'_c} = r \quad (6)$$

Eliminating  $I'_c$  from both equations, the optimal LAI ( $F_{\text{opt}}$ ) was derived:

$$F_{\text{opt}} = \frac{1}{K} \ln \frac{KI_0(b-ar)}{r(1-m)} \quad (7)$$

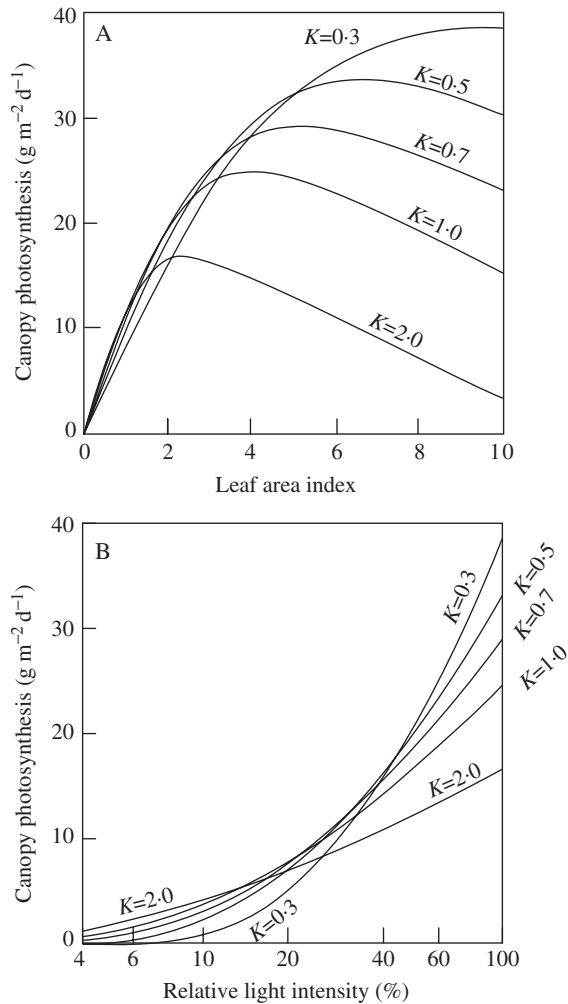


FIG. 2. (A) Daily canopy photosynthesis of a *Celosia cristata* stand under full daylight (100%) calculated from eqn (4), plotted as a function of leaf area index. Different  $K$ -values are assumed. (B) Daily maximum canopy photosynthesis as a function of relative incident radiation. Calculated from eqn (8) for different  $K$ -values. Redrawn after Saeki (1960).

Substitution of eqn (7) for  $F$  in (4) gives the maximal canopy photosynthesis [ $P_{\max} = P(F_{\text{opt}})$ ]:

$$P_{\max} = \frac{b}{aK} \ln \frac{1 + aKI_0/(1-m)}{1 + ar/(b-ar)} - \frac{r}{K} \ln \frac{KI_0(b-ar)}{r(1-m)} \quad (8)$$

This  $P_{\max}$  is plotted against the relative incident radiation for different  $K$ -values in Fig. 2B, which shows that a canopy with a small  $K$  responds to irradiance more strongly than one with a large  $K$ . At high irradiance canopy photosynthesis is maximized at a small  $K$ , whilst at low irradiance it is maximized at a larger  $K$ . These predictions are in agreement with our every-day experience: thick vegetation develops in open habitats, where most leaves are vertically inclined. In forest understoreys, we see flat leaves sparsely distributed in one layer. Kuroiwa (1971) proposed an ideal distribution of leaf angles in the canopy in which leaves change their angle from vertical at the top to horizontal at the bottom. However, many species in open habitats have leaf angles

more horizontal than the expectation from the optimization theory. Later, Hikosaka and Hirose (1997) showed that in an evolutionary stable pattern of leaf angles of individuals subject to competition, the leaves are more horizontal than would lead to maximal photosynthesis. In the period of the International Biological Programme (IBP, 1964–1974), the Monsi–Saeki theory was broadly applied to study primary production in a range of plant communities from grasslands to forests and from natural vegetation to agricultural crops (Monsi, 1968; Monsi *et al.*, 1973; Kira, 1975; Saeki, 1975).

The canopy photosynthesis model of Monsi and Saeki (1953) explained well the different stand structures that develop depending on a given light environment. However, some caveats should be stated here. First, the assumption that every leaf in the canopy has the same photosynthetic characteristics is not true. Sun and shade leaves differentiate within a stand and they have different photosynthetic capacities from each other (Boardman, 1977; Björkman, 1981). [McCree and Troughton (1966) suggested that the optimal LAI as assumed by Monsi and Saeki (1953) would not exist because shade leaves have a lower light compensation point.] However, Saeki (1959) noted that as the contribution of shaded leaves to total canopy photosynthesis was small, canopy photosynthesis calculated based on the photosynthesis of sun leaves gave virtually the same result as that calculated based on different photosynthetic capacities between sun and shade leaves. As will become clear from the remainder of this review, consideration of the photosynthetic capacity of leaves in different layers in the canopy provides new insights into canopy photosynthesis with respect to the resource use strategy of plants. The second caveat to be noted is that Monsi and Saeki (1953) assumed diffuse light (or overcast conditions, with parallel light coming from all directions) to derive eqn (1), on which their canopy photosynthesis model was built. Under sunny conditions, however, light distribution is more heterogeneous within the canopy: deep in the canopy, some leaves that receive sunflecks are sun-lit, whilst the others are shaded to different degrees. In such a situation, an assumption of overcast conditions over-estimates canopy photosynthesis, owing to the non-linearity of the light response of photosynthesis. The role of diffuse vs direct light on canopy photosynthesis was considered first by de Wit (1965) and Duncan *et al.* (1967), and has received renewed interest by Gu *et al.* (1999) and Roderick *et al.* (2001) (see Farquhar *et al.*, in later issue). The third caveat is that however well the ‘optimal’ LAI might explain the natural pattern observed, it must not be interpreted that the optimum has been realized at the stand level through natural selection. Individuals, not whole stands of vegetation, are the unit of natural selection (Williams, 1966). The optimal may be realized in isolated individuals and in those that produce a large canopy, such as clonal plants and trees, but not in individuals interacting and competing with each other (see Anten, 2005). Nonetheless, the theory and the concept of optimal LAI has a practical importance for agricultural management and the breeding of cultivars to increase crop yields (Loomis and Williams, 1969).

### COST–BENEFIT ANALYSIS OF RESOURCE USE

Mooney and Gulmon (1979) introduced the concept of costs and benefits in the study of resource use by plants with an econometric analogy. It is well known that there is a strong correlation between photosynthetic capacity and leaf nitrogen (Nair, 1975; Field and Mooney, 1986), because more than half of the nitrogen in a leaf is directly involved in photosynthesis (Evans, 1989; Evans and Seemann, 1989). The rate of photosynthesis increases with increasing protein content of a leaf. A question then arises: why don't all plants have high leaf-protein contents and hence high photosynthetic rates? Mooney and Gulmon (1979) answered this question by assuming costs in manufacturing proteins for photosynthetic carbon gains. In a light-limited habitat, photosynthesis saturates at a lower enzyme content than in a light-unlimited habitat (Fig. 3), indicating that plants growing in low light conditions should have leaves with low enzyme contents. Now assume that there are costs ( $C$ ) in manufacturing enzyme proteins ( $E$ ) and that the costs increase with increasing investment of proteins. To maximize net carbon gain [i.e. the difference between photosynthesis ( $P$ ) and  $C$ ,  $P - C$ ], the partial derivative of  $(P - C)$  with respect to  $E$  should equal to zero:  $\delta(P - C)/\delta E = 0$ . Then,

$$\frac{\delta P}{\delta E} = \frac{\delta C}{\delta E} \quad (9)$$

This equation defines the optimal amount of enzymes that should be invested within a leaf. The left- and right-hand sides of this equation are called 'marginal gain' and 'marginal cost', respectively. While marginal gain decreases with an increase in enzyme investment, plants should invest to the point at which the marginal cost (represented by the tangent lines in Fig. 3) exceeds the marginal gain. Note that the optimal enzyme content is smaller in a light-limited than in a light-unlimited habitat (Fig. 3).

Field (1983) formulated the allocation of leaf nitrogen for the maximization of carbon gain as

$$\frac{\delta p_{\text{day}}}{\delta n_L} = \lambda \quad (10)$$

where  $p_{\text{day}}$  is the daily carbon gain,  $n_L$  is leaf nitrogen per unit leaf area and  $\lambda$  is a constant. This equation may be derived from eqn (9) by substituting  $P$  and  $C$  for  $p_{\text{day}}$  and  $n_L$ , respectively, with the assumption that the marginal cost is constant. Since at high  $n_L$  the marginal gain is higher at high rather than at low irradiance, nitrogen should be allocated in the canopy such that leaves receiving the highest irradiance have the highest nitrogen per unit leaf area. Field (1983) applied this concept to a Californian chaparral shrub *Lepechinia calycina* and calculated daily carbon gain for different distributions of nitrogen in the canopy. However, profits from distributing nitrogen non-uniformly in the canopy were not large. The optimal distribution increased canopy photosynthesis by 3 % and the actual distribution increased it by 1 %, as compared with uniform distribution. Field suggested that 1–3 % benefits can be still larger than the cost involved in nitrogen redistribution (i.e. protein

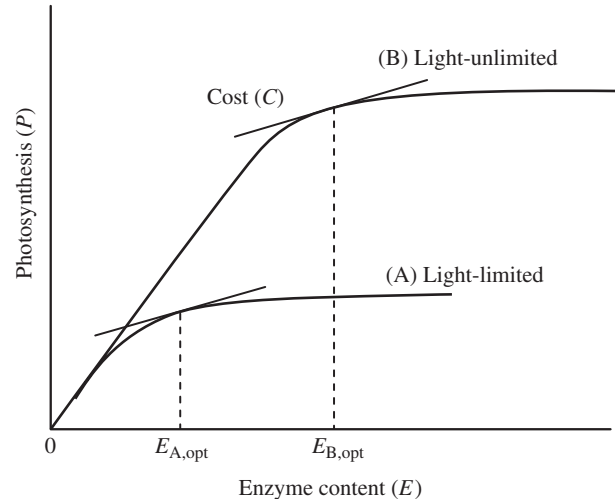


FIG. 3. Photosynthesis ( $P$ ) increases with increasing enzyme content ( $E$ ), but saturates at higher  $E$ . Saturation starts earlier in a light-limited (A) than light-unlimited (B) habitat. The slope of the tangent lines represents the cost ( $C$ ) of manufacturing one unit of enzyme. The tangent point defines the optimal enzyme investment ( $E_{A,\text{opt}}$  and  $E_{B,\text{opt}}$ ) that maximizes photosynthesis per enzyme content. See text for further explanation. Modified from Mooney and Gulmon (1979).

degradation, transport and loading of amino acids, and re-synthesis of proteins). Mooney *et al.* (1981) demonstrated that nitrogen redistribution is much more rapid in annual species native to closed-canopy habitats than in annuals of open habitats, implying that the potential importance of nitrogen distribution in the canopy increases with a larger gradient of irradiance. Assuming that photosynthetic capacity is linearly related to leaf nitrogen, Charles-Edwards *et al.* (1987) described a pattern of  $n_L$  that declines in proportion to the degree of shade within a canopy.

### LEAF NITROGEN DISTRIBUTION AND CANOPY PHOTOSYNTHESIS

Hirose and Werger (1987a, b) studied canopy photosynthesis in a *Solidago altissima* stand. This is a clonal species that produces many leaves along a tall stem without branching, and often makes a dense, pure stand in flood plains and in an abandoned fields (Iwaki *et al.*, 1969; Hirose, 1971; Kitamoto, 1972). Hirose and Werger (1987b) found that leaf nitrogen content per area ( $n_L$ ) decreased exponentially with increasing LAI cumulated from the top of the canopy ( $F$ ):

$$n_L = n_0 \exp\left(\frac{-K_a F}{F_t}\right) \quad (11)$$

where  $F_t$  is the total LAI,  $n_0$  is leaf nitrogen per area at the top of the canopy, and  $K_a$  is the coefficient of nitrogen allocation in the canopy.  $K_a = 0$  indicates a uniform distribution of nitrogen, in which every leaf has a nitrogen concentration equal to the mean.  $K_a$  increases with increasing non-uniformity of nitrogen distribution where upper leaves have higher nitrogen per unit leaf area than lower ones.

Hirose and Werger (1987b) modelled canopy photosynthesis of the *Solidago* stand, extending the Monsi–Saeki model with nitrogen distribution in the canopy being

TABLE 1. Predicted daily canopy photosynthesis for a *Solidago altissima* stand with uniform, actual and optimal nitrogen distributions among leaves.  $K_a$ , the coefficient of nitrogen allocation;  $P_{\text{day}}$ , daily canopy photosynthesis;  $n_L$ , nitrogen per leaf area.  $F_t = 4.24 \text{ m}^2 \text{ m}^{-2}$ ,  $N_t = 5.62 \text{ gN m}^{-2}$ ,  $\text{PPFD} = 43.2 \text{ mol m}^{-2} \text{ d}^{-1}$ . From Hirose and Werger (1987b)

	$K_a$	$P_{\text{day}}$ (mol CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup> )	$n_L$ (gN m <sup>-2</sup> )
Uniform	0	0.614 (100 %)	1.33
Actual	0.80	0.744 (121 %)	0.86–1.92
Optimal	1.30	0.781 (127 %)	0.65–2.37

taken into account. Leaf net photosynthesis ( $p$ ) as a function of PPFD ( $I'$ ) was described by a non-rectangular hyperbolic equation (Johnson and Thornley, 1984):

$$p = \frac{\phi I' + p_{\text{max}} - \sqrt{(\phi I' + p_{\text{max}})^2 - 4\theta\phi I' p_{\text{max}}}}{2\theta} - r \quad (12)$$

This equation includes four parameters:  $\phi$ , the initial slope;  $p_{\text{max}}$ , the light-saturated rate of photosynthesis;  $\theta$ , a curvature factor; and  $r$ , dark respiration. As these parameters were found to be a function of leaf nitrogen per area ( $n_L$ ), leaf net photosynthesis was calculated for a given leaf nitrogen under a given irradiance (Hirose and Werger, 1987a). Combining light [eqn (2)] and nitrogen [eqn (11)] distribution within the canopy and leaf photosynthesis as a function of light and nitrogen [eqn (12)] with a daily change in PPFD gave a daily canopy carbon gain.

Table 1 shows the effect of nitrogen distribution on daily canopy carbon gain. A large increase was found in actual and optimal nitrogen distribution as compared with uniform distribution. Non-uniform distribution benefited actual plants by 21 %, although the value was lower than the 27 % increase assumed by an optimal distribution. Large profits of non-uniform nitrogen distribution were demonstrated both in herbaceous species, *Lysimachia vulgaris* (27 % increase in actual over uniform distribution, Pons *et al.*, 1990) and *Carex acutiformis* (28 %; Werger and Hirose, 1991; Schieving *et al.*, 1992a), and in a broad-leaved evergreen tree *Nothofagus fusca* (6 %, Hollinger, 1996). Anten *et al.* (1995a) showed that profits from non-uniform distribution in actual plants were larger in dicots (41 % in *Glycine max* and 35 % in *Amaranthus cruentus*) than in monocots (14 % in *Oryza sativa* and 13 % in *Sorghum bicolor*). However, none of these plants attained the optimal N distribution. Actual plants distribute N more uniformly than the optimal distribution. Why didn't plants exhibit optimal N-distribution when this optimization would further enhance their carbon gain? A clue may be found in the range of nitrogen concentrations (see the last column in Table 1). The difference between actual and optimal distribution implies that optimal nitrogen distribution leads to leaf nitrogen per unit area that is too low at the bottom and too high at the top to be realized. Some nitrogen may not be capable of translocation, and a certain amount of nitrogen is necessary to utilize sunflecks that leaves receive in lower layers in the canopy (see Pons *et al.*, 1990). On the other hand, high

nitrogen may be risky: when plants are subjected to herbivory, they would lose a large amount of nitrogen at once (Stockhoff, 1994). Under a risk of herbivory, marginal costs increase with increasing nitrogen investment (Mooney and Gulmon, 1979).

Large returns from non-uniform distribution contrast with *Lepechinia calycina* where the effect of non-uniform distribution was small (see above; Field, 1983). The apparent disagreement between the result of Field and ours was solved by a model simulation. Hirose and Werger (1987b) calculated the daily carbon gain for different availabilities of nitrogen and leaf area index (Fig. 4). Leaf area as well as nitrogen availability were doubled or halved relative to those found in the *Solidago altissima* stand. Nitrogen was distributed either uniformly or optimally in the canopy. The effect of non-uniform distribution was larger in a dense than in an open stand. An open canopy showed a very small effect of 2–3 %, similar to the result of Field (1983). In reality, the Californian chaparral had an open canopy where the darkest microsite still received 20 % of full irradiance, which corresponds to LAI = 2.3 in our model. Plants in a dense stand benefit more from non-uniform distribution of nitrogen than those in an open stand, and dense canopies are expected to develop a steeper gradient of nitrogen than open canopies. In accordance with this expectation, a dense stand of *Lysimachia vulgaris* developed a steeper gradient of nitrogen than an open stand (Hirose *et al.*, 1988). At flowering and early seed ripening of *S. altissima*, part of the leaf nitrogen was translocated to reproductive structures. As a result less nitrogen was available for photosynthesis and lower leaves were dropped, with the remaining leaves being kept within the same range as before flowering and the gradient of leaf nitrogen becoming less steep (Werger and Hirose, 1988, 1991; Schieving *et al.*, 1992b). Leaf area index of the canopy appears to be the key regarding how nitrogen gradients will be set up. Strong gradients of nitrogen were found to develop in dense oak forest canopies (LAI up to 6; Wilson *et al.*, 2000), while most leaves had the same nitrogen in open oak savanna (LAI about 0.6; Xu and Baldocchi, 2003).

An important question raised from the optimal allocation theory is what controls nitrogen distribution within the canopy. As new leaves are produced at top of the plant, which is exposed to full irradiance, and as young leaves are usually high in protein content, leaf age was suggested to control the allocation program (Field, 1983; Field and Mooney, 1983), although the effect of ageing was different in extent between species native to closed habitats and those native to open canopy habitats (Mooney *et al.*, 1981). Hirose *et al.* (1989) studied nitrogen distribution in a stand of a monocotyledonous species, *Carex acutiformis*. As this species is a rosette plant having a meristem at the base of the plant, the youngest portion of a leaf blade is always subject to the lowest irradiance within the canopy. New leaf blades are produced in the centre and push older blades outwards, thus facilitating a comparison of nitrogen in leaf blades with different ages but exposed to the same light intensity. It was found that nitrogen distribution was correlated strongly with the light gradient in the canopy ( $r = 0.82\text{--}0.91$ ), with only a small effect of leaf age ( $r = 0.16\text{--}0.39$ ). Pons *et al.* (1993)

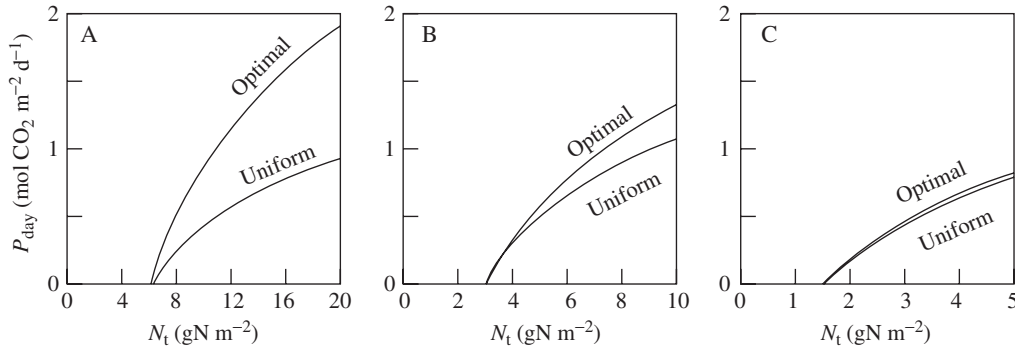


FIG. 4. Daily canopy photosynthesis ( $P_{\text{day}}$ ) versus total leaf nitrogen ( $N_t$ ) under the optimal and uniform nitrogen allocation program. The optimal allocation was determined by eqn (10). Note different scales on the x-axis. (A)  $F_t = 8.48 \text{ m}^2 \text{ m}^{-2}$ ; (B)  $4.24 \text{ m}^2 \text{ m}^{-2}$ ; (C)  $2.12 \text{ m}^2 \text{ m}^{-2}$ . From Hirose and Werger (1987b).

demonstrated that this species developed little gradient of nitrogen when leaves were illuminated uniformly from the top to bottom. Vines provide a useful material to study the control of leaf nitrogen, presenting leaves that can be exposed naturally or experimentally to different irradiance independently of leaf age. Ackerly (1992) found that leaf nitrogen in a tropical vine *Synogonium podophyllum* was more strongly determined by light than by leaf age. Hikosaka *et al.* (1994) subjected a vine *Ipomoea tricolor* to reverse canopy-type shading (progressively shading younger leaves) and found the more illuminated older leaves had a higher leaf nitrogen per area than the more shaded younger leaves. The importance of irradiance rather than age in determining leaf nitrogen was also shown in individuals with different heights in a dense stand (Anten and Werger, 1996; Anten *et al.*, 1998; for review, Anten *et al.*, 2000; but see Kitajima *et al.*, 2002, 2005).

Theoretically, canopy photosynthesis is maximized when each leaf in the canopy receives irradiance in proportion to the associated photosynthetic capacity (Farquhar, 1989; see also Terashima *et al.*, 2005):

$$P_{\text{max}1} : P_{\text{max}2} : P_{\text{max}3} : \dots = I'_1 : I'_2 : I'_3 : \dots \quad (13)$$

where 1, 2, 3, ... indicate different leaves. Assuming that the photosynthetic capacity is proportional to the amount of nitrogen directly involved in photosynthesis, Anten *et al.* (1995a) derived the optimal nitrogen distribution:

$$n_L = \frac{K(N_t - n_b F_t) e^{-KF}}{1 - e^{-KF}} + n_b \quad (14)$$

where  $N_t$  is the total amount of leaf canopy nitrogen,  $F_t$  is the total LAI, and  $n_b$  is the leaf nitrogen per area that is not involved in photosynthesis. Equation (14) indicates that the photosynthetic nitrogen ( $n_L - n_b$ ) decreases exponentially as a function of  $F$  where the proportionality constant is  $K$ , the light extinction coefficient [see eqn (1)]. Nitrogen distribution is primarily determined by the structure of the canopy ( $K$ ), by the availability of nitrogen ( $N_t$ ), and by the amount of nitrogen invested to structural components of the leaf ( $n_b$ ). It is independent of leaf physiology and the absolute amount of photons that plants receive. Reduction in

$n_L$  with increasing depth in the canopy has been observed both in agricultural crops and wild plants, and in both herbaceous and woody species (Grindlay, 1997).

These experimental and theoretical studies supported the hypothesis that the gradient of leaf nitrogen that develops in a canopy is a direct response to the gradient of light. Leaf age plays a secondary role in the development of the gradient of leaf nitrogen. The gradient benefits plants through the efficient use of light and nitrogen, two resources whose supply is limiting in the natural environment. Chen *et al.* (1993) proposed the co-ordination theory to explain nitrogen distribution in a canopy. It assumed that photosynthesis is limited by either the RuBPCase-limited rate of carboxylation ( $W_c$ ) or the electron transport-limited rate of carboxylation ( $W_j$ ) and that at a given light level there is a unique  $n_L$  at which photosynthesis is co-limited by  $W_j$  and  $W_c$ . This co-ordination theory may explain  $n_L$  decreasing with increasing depth in the canopy, but does not explain  $n_L$  that changes depending on nitrogen availability as well. Optimization theory, on the other hand, predicts that  $n_L$  should be distributed in proportion to light levels, and thus the distribution depends both on light and nitrogen availability in the canopy [eqn (14)].

Hikosaka and Terashima (1995) applied the optimization theory for studying light acclimation of leaf photosynthesis. They determined the pattern of N partitioning among photosynthetic components in chloroplasts that maximizes the daily carbon gain for various light environments and leaf N contents. At high irradiance, nitrogen should be allocated more to Calvin cycle enzymes and electron carriers, whilst at low irradiance, it is allocated relatively more to chlorophyll–protein complexes. Thus modelling of canopy photosynthesis with leaf nitrogen distribution enables us to scale up from chloroplast biochemistry to canopy carbon gain (Farquhar, 1989; Kull and Jarvis, 1995; Terashima and Hikosaka, 1995; De Pury and Farquhar, 1997). On the canopy photosynthesis model, Hikosaka (2003) developed a new model of leaf and nitrogen dynamics in a canopy (see Hikosaka, 2005). Canopy photosynthesis models were further applied for studying the strategy of resource use in species and individuals growing at different light and nitrogen availabilities (see below). Links between photosynthesis, nitrogen and light climate have also been implied

in global-scale vegetation patterns (Reich *et al.*, 1997; Niinemets, 2001) and used for global carbon exchange between vegetation and the atmosphere (Friend, 2001).

### CANOPY STRUCTURE OF PLANT COMMUNITIES WITH MANY SPECIES

Most plant communities in the natural environment are composed of a range of species differing considerably in plant height. Tall dominant species occupy upper layers and receive a high irradiance, while short subordinate species receive a low irradiance. Here we may have two hypotheses: species in upper layers are limited by the availability of nitrogen rather than by the irradiance, and species in the lower layers are limited by the irradiance rather than the nitrogen availability. We may then expect a high nitrogen use efficiency and consequently a relatively low  $n_L$  in the species in the upper layers. On the other hand, the cost-benefit hypothesis for nitrogen use predicts a high  $n_L$  in the dominant species and a low  $n_L$  in the subordinate species in the canopy.

Hirose and Werger (1994, 1995) studied a herbaceous plant community (Thelypterido–Phragmitetum) that contained 11 species in a small area. *Phragmites australis* developed leaves in the uppermost layer, *Calamagrostis canescens* and *Carex acutiformis* in the next layer, and the other eight species were living in lower layers. The upper three species, comprising 95 % of the total leaf area, dominated the stand. The other eight species together had only 5 % of the total leaf area. How can those smaller species survive if they receive only small amounts of light? Hirose and Werger calculated the photon flux (number of photons per unit time) absorbed by each species ( $\Phi$ ) from its leaf area distribution in the gradient of light in the canopy, determined by the stratified clipping technique (Monsi and Saeki, 1953). They defined  $\Phi_N$  as the ratio of photon flux absorption to leaf nitrogen ( $N$ ):

$$\Phi_N = \frac{\Phi}{N} \quad (15)$$

Leaves need both photons and nitrogen for photosynthetic carbon gain, and the cost-benefit theory predicted that nitrogen would be partitioned among species in proportion to the amount of absorbed photons (Anten *et al.*, 1995a). If the photosynthetic rate is proportional to the amount of absorbed photons,  $\Phi_N$  indicates *in situ* photosynthetic nitrogen use efficiency (photosynthesis per unit leaf nitrogen; Field and Mooney, 1986). Dividing both the numerator and denominator of eqn (15) by leaf area in each species, we have

$$\Phi_N = \frac{\Phi_{\text{area}}}{n_L} \quad (16)$$

where  $\Phi_{\text{area}}$  is the photon absorption per unit leaf area. When  $\Phi_N$  and  $n_L$  are plotted logarithmically on the  $y$ - and  $x$ -axis, respectively,  $\Phi_N$  is given as parallel contours with a slope of 1 (Fig. 5). Across species there was a positive correlation between  $\Phi_{\text{area}}$  and  $n_L$  ( $r = 0.54$ ,  $P < 0.1$ ). Nitrogen was partitioned between species such that those

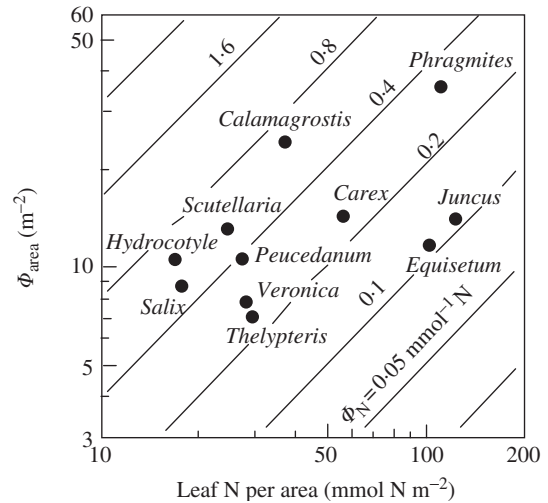


FIG. 5. Photon absorption per unit leaf area ( $\Phi_{\text{area}}$ ,  $y$ -axis), leaf nitrogen per unit area ( $n_L$ ,  $x$ -axis) and photon absorption per unit leaf nitrogen ( $\Phi_N$ , contours) of 11 species in the canopy of the Thelypterido–Phragmitetum.  $\Phi_N = \Phi_{\text{area}}/n_L$ . Relative values for  $\Phi$ . From Hirose and Werger (1994).

capturing a large amount of photons had high nitrogen per leaf area. This is consistent with the prediction of the cost-benefit hypothesis. Dominants captured a higher irradiance with leaves of higher nitrogen content per area, as compared to subordinate species. Subordinates received a lower fraction of irradiance, but their nitrogen use efficiency was not smaller than those of dominants. Note that subordinates with photosynthetic stems instead of leaves (*Juncus* and *Equisetum*) are outliers.  $n_L$  is the ratio of leaf nitrogen per mass ( $n_{LM}$ ) to the specific leaf area ( $\sigma$ , leaf area per unit leaf mass):

$$n_L = \frac{n_{LM}}{\sigma} \quad (17)$$

Within a species,  $n_L$  changed responding to irradiance and the difference in  $n_L$  was caused by  $n_{LM}$  rather than by  $\sigma$ , whereas difference in  $n_L$  between species was caused mainly by different  $\sigma$  (Hirose and Werger, 1994). Different photosynthetic capacities between species growing different layers have been documented in a deciduous forest (Kull and Niinemets, 1998).

Plants develop above-ground structures to competitively capture photons as an energy source. Tall dominant species capture a greater fraction of incident radiation, while shorter subordinate species receive a smaller fraction but nevertheless co-exist with taller species. In what characters do tall species differ from subordinate species as regards the exploitation of light resources, and are there any possible selective advantages in the characters of subordinate species? Hirose and Werger (1995) defined the absorption of photons per unit above-ground mass:

$$\Phi_{\text{mass}} = \frac{\Phi}{M} \quad (18)$$

where  $M$  is plant above-ground mass. If the above-ground mass is considered as a cost to capture photons, then this ratio indicates an efficiency of biomass use for capturing photons. There was some variation in  $\Phi_{\text{mass}}$  among species

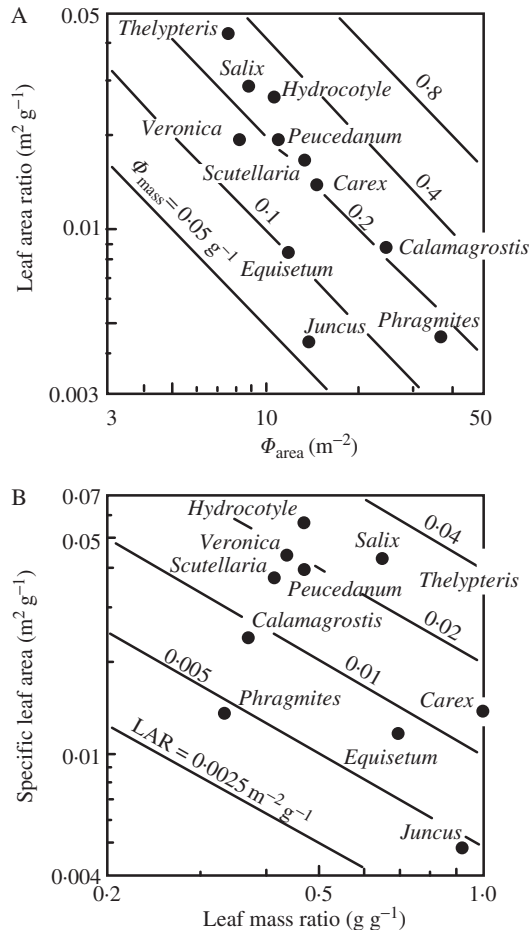


FIG. 6. (A) Photon absorption per unit leaf area ( $\Phi_{area}$ , x-axis), leaf area ratio ( $A_M$ , y-axis) and photon absorption per unit above-ground mass ( $\Phi_{mass}$ , contours) of species in the canopy of the *Thelypteris*-*Phragmites*.  $\Phi_{mass} = \Phi_{area} \times A_M$ . Relative values for  $\Phi$ . (B) Leaf mass ratio ( $f_{LM}$ , x-axis), specific leaf area ( $\sigma$ , y-axis) and leaf area ratio ( $A_M$ , contours) of species.  $A_M = f_{LM} \times \sigma$ . From Hirose and Werger (1995).

but, surprisingly, no significant difference was found in  $\Phi_{mass}$  between dominant and subordinate species as groups. Subordinate species absorbed much smaller amounts of photons, but their efficiencies were similar to or even higher than dominant species. Then the next question is how the subordinate species attained their high  $\Phi_{mass}$ .

Dividing both the numerator and denominator of eqn (18) by leaf area,  $\Phi_{mass}$  was separated into two components:

$$\Phi_{mass} = \Phi_{area} \times A_M \quad (19)$$

$A_M$  is the leaf area ratio (ratio of leaf area to above-ground mass). When  $A_M$  and  $\Phi_{area}$  are plotted logarithmically on the y- and x-axis, respectively,  $\Phi_{mass}$  is given by contours (Fig. 6A). Across species there was a negative correlation between the two axes ( $r = 0.78$ ,  $P < 0.01$ ). Dominants captured high light by placing leaves at higher positions in the canopy using the investment of a large amount of biomass into supporting tissues and thus reducing  $A_M$ , while subordinates receive low light but with a high  $A_M$  resulting from a limited investment in support tissues. A decrease in

the fraction of biomass in leaves with increasing plant height has been documented among understorey herbs (Givnish, 1982).  $A_M$  was further separated into leaf mass ratio ( $f_{LM}$ , fraction of above-ground mass in leaf mass) and  $\sigma$ :

$$A_M = f_{LM} \times \sigma \quad (20)$$

Subordinate species attained a high  $A_M$  by having a high  $\sigma$  rather than a high  $f_{LM}$  (Fig. 6B). In a mixed-species stand, dominant and subordinate species are different in the amount of resources they acquire, but may not be different in the efficiency of resource use, allowing them to co-exist in the stand (Hirose and Werger, 1995; Anten and Hirose, 1999). Different strategies of biomass allocation have been suggested in forest ecosystems, where upper-storey species allocate more biomass to height growth and understorey species more to lateral growth (Kohyama, 1987; King, 1990). Sakai (1991) showed that herbs develop different architectures (clonal growth forms) as a result of competition in habitats with different openness and crowding conditions.

Anten and Hirose (2003) studied canopy photosynthesis in a grassland inhabited by both C3 and C4 species. C4 species dominated at the site with their higher photosynthetic capacity. Sensitivity analysis showed that the C4 metabolism benefited the dominant species but would not benefit understorey species. Studies of canopy photosynthesis in stands with many species are limited in number. Wohlfahrt *et al.* (1998, 2001) modelled leaf  $CO_2$  exchange for species in mountain grassland ecosystems and incorporated the results into their vegetation-atmosphere  $CO_2$  and energy-exchange model. The model prediction of canopy net photosynthesis was verified with independent above-canopy measurements of  $CO_2$  and energy exchange.

#### SIZE STRUCTURE OF POPULATIONS IN THE PLANT COMMUNITY

There is a large variation in size among individuals in a stand. According to Koyama and Kira (1956), size inequality increases when the growth rate is disproportionately larger in larger individuals, but it does not change when the growth rate of individuals is proportional to their size. Competition among individuals in a stand is usually asymmetric or one-sided, where larger individuals obtain a disproportionate share of the resources and suppress the growth of smaller individuals (Weiner, 1990; Hara, 1992; Nagashima, 1999). However, there have been few studies that directly demonstrate that competition among individuals is asymmetric (but see Weiner, 1986). Anten and Hirose (1998) applied the concept of  $\Phi_{mass}$  to individuals in a monospecific stand of *Xanthium canadense*, and showed that tall dominant individuals captured light resources more than proportionately to their size. Tall plants having higher  $\Phi_{mass}$  were competitively more successful than smaller plants (see fig. 7 in Anten, 2005—this issue). Small individuals responded to low light by increasing  $A_M$ , but owing to developmental constraints the plastic increase in  $A_M$  was not



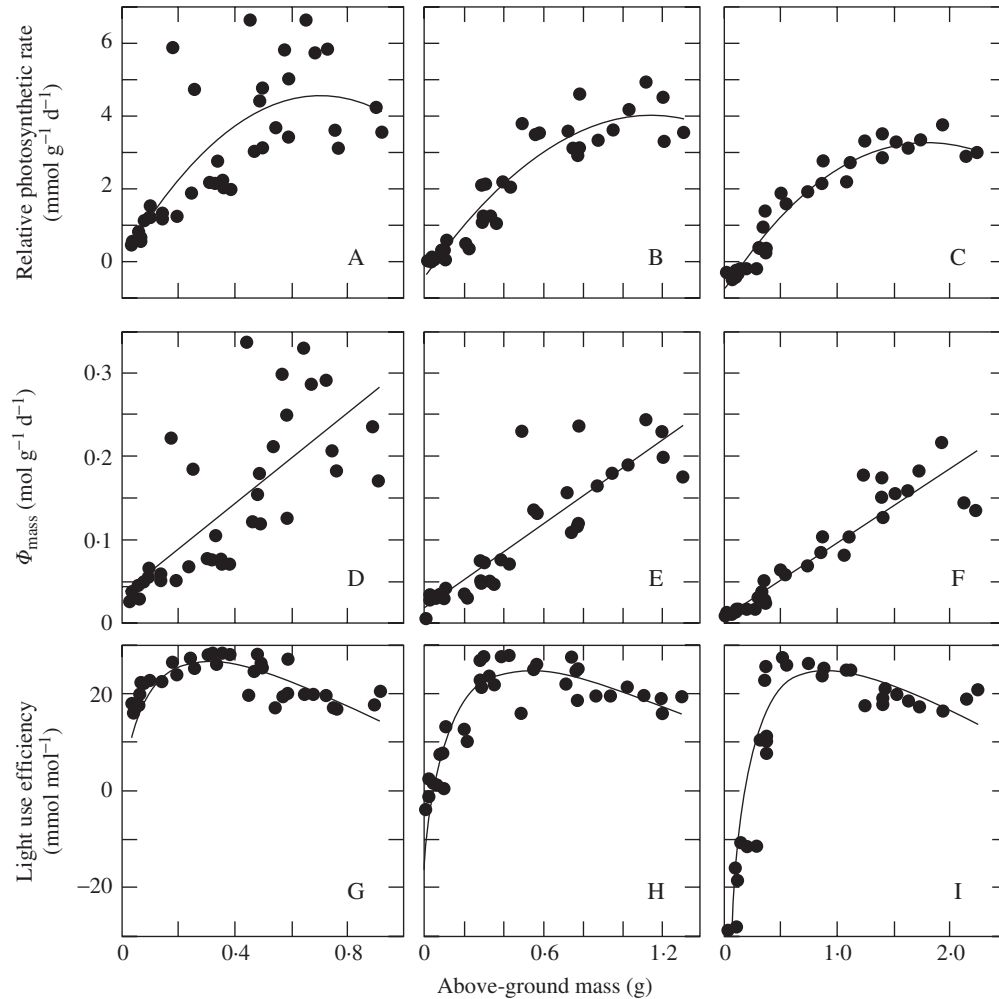


FIG. 7. (A–C) Relative photosynthetic rate ( $R$ , daily net photosynthesis per unit above-ground mass), (D–F) daily photon absorption per unit above-ground mass ( $\Phi_{\text{mass}}$ ), and (G–I) light use efficiency ( $\epsilon$ , net photosynthesis per unit photon absorption) as a function of above-ground mass of individuals in a *Xantium canadense* stand. Note that  $R = \Phi_{\text{mass}} \times \epsilon$ . (A, D, G) 22 July; (B, E, H) 1 August; (C, F, I) 11 August. From Hikosaka *et al.* (1999).

large enough to compensate for the low  $\Phi_{\text{area}}$ . This is quite different from the pattern observed among species in multi-specific stands where  $\Phi_{\text{mass}}$  was not different between dominant and subordinate species (Fig. 6A; Hirose and Werger, 1995). Therefore, it may be concluded that individuals (having different  $\Phi_{\text{mass}}$ ) in a monospecific stand compete for light, while different species (having similar  $\Phi_{\text{mass}}$ ) in a multi-specific stand tend to co-exist with each other (see also Anten and Hirose, 1999, 2001, 2003).

Hikosaka *et al.* (1999) determined the growth of individuals in a dense stand of *X. canadense* by applying the canopy photosynthesis model to individual plants. Relative photosynthetic rate ( $R$ , photosynthetic rate per unit above-ground mass, a surrogate for the relative growth rate) was a saturating function of plant mass, indicating overall asymmetric competition between individuals and symmetric competition between large individuals (Fig. 7A–C).  $R$  is a product of  $\Phi_{\text{mass}}$  and the light use efficiency ( $\epsilon$ , net carbon gain per unit photon absorption):

$$R = \Phi_{\text{mass}} \times \epsilon \quad (21)$$

This equation implies that plant growth is determined by the efficiency of light use in photosynthesis as well as by the amount of light acquisition.  $\Phi_{\text{mass}}$  was higher in larger individuals (Fig. 7D–F), while  $\epsilon$  was highest in individuals with intermediate above-ground mass (Fig. 7G–I).

Berendse and Aerts (1987) defined nitrogen use efficiency (net carbon gain per unit nitrogen loss) as a product of the nitrogen productivity (Ingestad, 1979) and the mean residence time of nitrogen. Applying this concept to individuals in the stand of *X. canadense*, Hikosaka and Hirose (2001) showed that the nitrogen use efficiency was higher in dominants than in subordinates and that it was caused by a higher nitrogen productivity and a longer residence time of nitrogen in the former. They also showed that competition for nitrogen was less asymmetric between individuals than that for light. In a beech forest, Yasumura *et al.* (2002) found that canopy and understorey species were not different in leaf-level nitrogen use efficiency, where the high nitrogen productivity in the canopy species was offset by the low mean residence time of nitrogen.

## CONCLUDING REMARKS

In this paper I have shown how Monsi and Saeki (1953) developed their theory from the work of Boysen Jensen (1932), and how the model of Monsi and Saeki was furthered with the cost–benefit hypothesis in resource use advocated by Mooney and co-workers (1979–1983). A new method was introduced to study multi-specific stands with respect to resource partitioning among species (Hirose and Werger, 1994, 1995). This method was subsequently applied to the analysis of resource acquisition and its use by individuals in the stand. One of the directions that Monsi and Saeki (1953) suggested but which has not been fully addressed is an analysis of species' replacement in plant communities. Monsi and Saeki (1953; their fig. 8) beautifully described a drama of seasonal replacement of species in the Tajimagahara plain: *Sanguisorba tenuifolia* started growth early in spring and dominated the stand but was soon over-shaded by *Phragmites australis*, which grew later but taller with a large rhizome system below ground. *Phragmites* nearly monopolized the stand in the summer through to the autumn, but this monopolization ended with a cover of vines. We may apply the concept of resource acquisition and use to quantitatively describe the mechanism of species replacement. Monsi and Oshima (1955) theoretically analysed the process of plant succession after gap formation in a forest. Recently Werger *et al.* (2002) studied the process of regeneration and species' replacement after excluding sika deer from a grazing sward. They analysed the process of taller species replacing shorter grazing-tolerant ones with respect to the species' strategy of biomass allocation for light capture.

With the rise in the atmospheric CO<sub>2</sub> concentration, the role of terrestrial ecosystems in the global carbon cycle becomes a critical issue (Canadell *et al.*, 2000). Canopy photosynthesis models have been extended to evaluate the potential of terrestrial carbon fixation (Cramer *et al.*, 1999). Ecosystem carbon exchanges are being assessed extensively with the new technique of eddy covariance (FLUXNET; Aubinet *et al.*, 2000; Baldocchi, 2003). Tests of canopy photosynthesis models with eddy covariance data have shown that the models are producing accurate estimates of canopy photosynthesis on multiple time-scales for complex forest and crop canopies (Ruimy *et al.*, 1995; Kramer *et al.*, 2002). Canopy photosynthesis models are useful to predict the effect of elevated CO<sub>2</sub> on canopy structure and function (e.g. Koch and Mooney, 1996). High CO<sub>2</sub> may benefit leaves by enabling them to photosynthesize at a low irradiance, because the light compensation point decreases due to an increase in the initial slope (Ehleringer and Björkman, 1977; Long and Drake, 1991). The Monsi–Saeki theory on the optimal LAI suggests that the LAI would increase in a high-CO<sub>2</sub> world. Hence, Oikawa (1987) suggested a possibility that species' diversity reduces in understorey vegetation with lowered light availabilities. Nagashima *et al.* (2003) demonstrated that elevated CO<sub>2</sub> benefited dominant individuals more than subordinates and consequently increased size inequality, and Hikosaka *et al.* (2003) analysed the mechanisms involved in the development of hierarchy. However, Hirose

*et al.* (1996) have shown that LAI would not increase unless nitrogen availability increased simultaneously, because the increase in the initial slope makes leaves in lower layers more nitrogen-limited (Hirose *et al.*, 1997; see also Anten *et al.*, 1995b). The process-based mechanistic models of canopy photosynthesis initiated by Monsi and Saeki (1953) will become more useful than ever to analyse vegetation processes and to predict future ecosystems.

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