

REVIEW

## Leaf Canopy as a Dynamic System: Ecophysiology and Optimality in Leaf Turnover

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Received: 21 July 2003 Returned for revision: 6 November 2003 Accepted: 13 April 2004 Published electronically: 7 December 2004

• *Background and Aims* In a leaf canopy, there is a turnover of leaves; i.e. they are produced, senesce and fall. These processes determine the amount of leaf area in the canopy, which in turn determines canopy photosynthesis. The turnover rate of leaves is affected by environmental factors and is different among species. This mini-review discusses factors responsible for leaf dynamics in plant canopies, focusing on the role of nitrogen.

• *Scope* Leaf production is supported by canopy photosynthesis that is determined by distribution of light and leaf nitrogen. Leaf nitrogen determines photosynthetic capacity. Nitrogen taken up from roots is allocated to new leaves. When leaves age or their light availability is lowered, part of the leaf nitrogen is resorbed. Resorbed nitrogen is re-utilized in new organs and the rest is lost with dead leaves. The sink–source balance is important in the regulation of leaf senescence. Several models have been proposed to predict response to environmental changes. A mathematical model that incorporated nitrogen use for photosynthesis explained well the variations in leaf lifespan within and between species.

• *Conclusion* When leaf turnover is at a steady state, the ratio of biomass production to nitrogen uptake is equal to the ratio of litter fall to nitrogen loss, which is an inverse of the nitrogen concentration in dead leaves. Thus nitrogen concentration in dead leaves (nitrogen resorption proficiency) and nitrogen availability in the soil determine the rate of photosynthesis in the canopy. Dynamics of leaves are regulated so as to maximize carbon gain and resource-use efficiency of the plant.

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**Key words:** Canopy photosynthesis, canopy structure, cost–benefit analysis, evolutionarily stable strategy, leaf area index, leaf lifespan, leaf senescence, leaf turnover, nitrogen resorption, nitrogen turnover, nitrogen use efficiency, optimality model.

### INTRODUCTION

At the ecosystem level, leaf canopy is the unit of photosynthesis. Photosynthetic rates of the canopy vary depending on climate and on structure and physiology of individuals in the canopy. Understanding factors that affect canopy photosynthesis would contribute to agriculture, ecology, meteorology, and global science.

Leaf area distribution is an important determinant of rates of photosynthesis in the canopy (Monsi and Saeki, 1953). When the leaf area index (LAI; leaf area per unit ground area) increases, photon flux density (PFD) captured by the canopy increases, leading to higher photosynthetic production in the canopy. However, when leaves at the bottom receive PFD that is lower than the compensation point of photosynthesis, further increase in LAI decreases canopy photosynthesis. There is an optimal LAI that maximizes rates of photosynthesis (Monsi and Saeki, 1953; Saeki, 1960). Leaf nitrogen is another important factor for canopy photosynthesis. Since about half of leaf nitrogen is invested in photosynthetic proteins, there is a strong correlation between the photosynthetic capacity (the light-saturated rate of photosynthesis at an ambient condition) and leaf nitrogen content per unit area (Field and Mooney, 1986; Evans, 1989a). Thus, to have high rates of photosynthesis, canopies should accumulate a large amount of nitrogen in their leaves (Hirose and Werger, 1987b).

Neither LAI nor nitrogen content of the canopy is a static parameter, but changes dynamically with canopy growth. A

leaf canopy can be regarded as a population of leaves (Harper, 1989). Leaves are produced and senesce with a certain lifespan. When the canopy is young, the number of produced leaves is larger than that of senescing leaves. When the canopy is mature the turnover of leaves may be close to steady state. Similarly, nitrogen is taken up from soil and is lost with dead leaves. Standing LAI and nitrogen content are a result of the turnover of leaves and nitrogen.

Here is a review of the dynamics of leaf area and nitrogen in leaf canopies. In the first part, two components of leaf turnover—leaf production and senescence—are discussed in relation to canopy photosynthesis. The discussion is focused, particularly, on the role of nitrogen. It has been argued that plants regulate leaf longevity so as to maximize their fitness (Chabot and Hicks, 1982; Kikuzawa, 1991). Then in the second part, leaf turnover is discussed with regard to its optimization.

### ECOPHYSIOLOGY OF LEAF TURNOVER

#### *Leaf production*

Pattern of leaf production varies among species. Most annual herbs and many tropical pioneer trees produce their leaves continuously during vegetative growth (Ackerly, 1996; Kikuzawa, 2003), whereas many deciduous trees and shrubs produce leaves simultaneously at the beginning of the growing season without later leaf production (Kikuzawa, 1983, 2003). Kikuzawa (1983, 1984) categorized the pattern of leaf production into flush, succeeding and

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intermediate types. When species with similar growth forms are compared, the flush type is usually found in species with a longer leaf lifespan (Koike, 1988; Reich, 1993).

The rate of leaf area production,  $G_{\text{can}}$  ( $\text{m}^2 \text{m}^{-2} \text{d}^{-1}$ ) may be defined as follows:

$$G_{\text{can}} = P_{\text{can}} \times A_{\text{L}} \times C_e / M \quad (1)$$

where  $P_{\text{can}}$  is the rate of canopy photosynthesis per unit ground area ( $\text{mol C m}^{-2} \text{d}^{-1}$ ),  $A_{\text{L}}$  is the fraction of assimilates allocated for leaf construction,  $C_e$  is the conversion efficiency from assimilates to biomass ( $\text{g mol}^{-1} \text{C}$ ) and  $M$  is leaf mass per area (LMA) of new leaves ( $\text{g m}^{-2}$ ) (Ackerly, 1996; Hikosaka, 2003). Equation (1) assumes the succeeding type of leaf production, but it is also applicable to the flush type if the average production rate is calculated for a longer period than the interval of flushes. Note that this equation does not necessarily indicate the production rate of individual leaves. When plants produce leaves with a smaller size under less productive conditions,  $G_{\text{can}}$  becomes lower even when the rate of individual leaf production is constant.

According to the canopy photosynthetic model, the rate of photosynthesis in the canopy ( $P_{\text{can}}$ ) is determined by three factors: vertical profile of PFD in the canopy, LAI and photosynthetic capacity of leaves in the canopy (Monsi and Saeki, 1953; see Hirose, 2005).  $A_{\text{L}}$  is sensitive to changes in the environment of the plant. For example, nitrogen deficiency decreases  $A_{\text{L}}$  with increased allocation of biomass to roots (Brouwer, 1962; Hirose, 1987; Wilson, 1988). This is regarded as an adaptive response to compensate for low rates of nitrogen uptake. As the plant height increases, the ratio of leaf to stem mass may decrease to maintain mechanical stability (McMahon, 1973; Givnish, 1982).

LMA is different among species. Higher LMA is found in species with an inherently slow growth rate (Poorter and Remkes, 1990; Poorter and Evans, 1998) and with a longer leaf lifespan (Reich *et al.*, 1991, 1992, 1997, 1999), and may be a factor leading to lower productivity (see eqn 1). However, an increase in LMA has been shown to contribute to leaf toughness, suggesting that higher LMA is necessary to maintain leaves for a longer period (Reich *et al.*, 1991; Wright and Cannon, 2001; Wright and Westoby, 2002). Within a species, LMA is sensitive to environmental conditions, especially to light availability. Sun leaves generally have a higher LMA than shade leaves to accommodate more chloroplasts per unit leaf area (Björkman, 1981; Terashima *et al.*, 2001; Oguchi *et al.*, 2003).

The inverse of  $C_e$  is the construction cost of a leaf. Construction cost has been estimated with several methods. One is based on the relationship between respiration and growth (Merino *et al.*, 1982). When the specific respiration rate is plotted against the relative growth rate, the relationship is a linear function with a positive  $Y$ -intercept (Thornley, 1970; Kimura *et al.*, 1978). The intercept gives the maintenance respiration rate and the slope the conversion efficiency from glucose (respiratory substrate) to biomass. The other method uses construction costs of leaves (glucose equivalent) calculated from the chemical composition (Penning

de Vries *et al.*, 1974; McDermitt and Loomis, 1982; Chapin, 1989) or determined from the heat of combustion (Williams *et al.*, 1987). Many authors studied the interspecific variation in  $C_e$  to test the hypothesis that leaves with a longer lifespan may have a high  $C_e$  because of costly compounds for chemical defense or physical toughness (Coley *et al.*, 1985). However, they failed to find a clear difference in  $C_e$  among leaves with different lifespans, or between evergreen and deciduous leaves. None of the following are correlated with leaf lifespan: the slope of the relationship between respiration and growth (Merino *et al.*, 1982); the construction cost calculated from its chemical composition (Chapin, 1989); or the heat of combustion (Williams *et al.*, 1989). Compiling data of the heat of combustion from 203 woody species, however, Poorter and Villar (1997) found a small but significant difference between evergreen and deciduous leaves. Similar results were obtained in a literature survey by Villar and Merino (2001). Navas *et al.* (2003) also found a weak but significantly positive correlation between lifespan and construction cost of leaves among Mediterranean species. Similar values of construction cost in leaves with a different leaf lifespan may have come from a trade-off between costly chemicals. Leaves with a longer lifespan tend to accumulate carbon-based secondary compounds such as phenolics, while those with a shorter lifespan contain a large amount of proteins (Chapin, 1989; Poorter and Villar, 1997).

#### Nitrogen allocation to leaves

Nitrogen is one of the elements most limiting plant growth in many ecosystems (Aerts and Chapin, 2000). This is partly because plants need a large amount of nitrogen for photosynthesis. About half of leaf nitrogen is invested in the photosynthetic apparatus (Evans and Seemann, 1989; Hikosaka and Terashima, 1996). Within a species, there is a strong correlation between the photosynthetic capacity and nitrogen content of a leaf (Makino *et al.*, 1983; Hirose and Werger, 1987a; Evans, 1989a) and the rate of photosynthesis in a canopy increases as its nitrogen content increases (Hirose and Werger, 1987b).

Within a canopy, plants allocate nitrogen among leaves such that leaves exposed to higher PFDs have higher nitrogen contents (Field, 1983; Hirose and Werger, 1987b; Hirose *et al.*, 1988; Hollinger, 1989; Ellsworth and Reich, 1993; Niinemets, 1997; Osada *et al.*, 2003). At a high PFD, a greater investment of nitrogen increases photosynthetic production while, at a low PFD, rates of photosynthesis respond little to nitrogen content (Hirose and Werger, 1987a). Thus as PFD increases the optimal nitrogen content that maximizes photosynthetic productivity per unit nitrogen increases (Hirose and Werger, 1987a; Hikosaka and Terashima, 1995; Terashima and Hikosaka, 1995). Theoretical models have shown that a non-uniform allocation of leaf nitrogen leads to efficient use of nitrogen in canopy photosynthesis (Pons *et al.*, 1989; Schieving *et al.*, 1992; Evans, 1993; Anten *et al.*, 1995a).

The slope of the photosynthesis–nitrogen relationship is different among species (Field and Mooney, 1986; Evans, 1989a). Since leaf nitrogen content per unit area is not very

different among species (Reich *et al.*, 1991, 1992, 1999), the slope, which is intimately related to the photosynthetic nitrogen use efficiency (PNUE, photosynthetic capacity per unit leaf nitrogen), is the most important factor for the interspecific difference in photosynthetic capacity. PNUE has been studied as an inherent trait of species (Pons *et al.*, 1994). It has been shown that less steep slopes of the photosynthesis–nitrogen relationship tend to be found in tree species rather than in herbs (Evans, 1989a; Hikosaka *et al.*, 1998), in C<sub>3</sub> than in C<sub>4</sub> species (Sage and Percy, 1987; Anten *et al.*, 1995a), in slow-growing species (Poorter *et al.*, 1990; Pons *et al.*, 1994), in species with a long leaf lifespan (Reich *et al.*, 1992), in species inhabiting high altitudes (Westbeek *et al.*, 1999; Hikosaka *et al.*, 2002), and in species with a high LMA (Poorter and Evans, 1998). Variation in the slope is caused by several factors such as nitrogen allocation to the photosynthetic apparatus, the specific activity of photosynthetic enzymes, and conductance for CO<sub>2</sub> diffusion from air to chloroplasts (Lloyd *et al.*, 1992; Hikosaka *et al.*, 1998; Poorter and Evans, 1998; Westbeek *et al.*, 1999).

Why do some species have a low PNUE? A negative relationship between PNUE and LMA implies that investments in physical toughness sacrifices PNUE (Reich *et al.*, 1991; Pons *et al.*, 1994; Hikosaka *et al.*, 1998). Recently, Takashima *et al.* (2004) determined nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. They found that evergreen species allocate more nitrogen to cell wall proteins at the expense of nitrogen allocation to the photosynthetic apparatus. Onoda *et al.* (2004) found that *Polygonum cuspidatum*, a perennial herb, alters nitrogen allocation in leaves depending on the germination time such that early germinators invest more nitrogen in cell wall proteins and less to photosynthetic proteins. In both studies, the fraction of leaf nitrogen allocated to cell walls was positively correlated with leaf mass per area. There may be a trade-off in nitrogen partitioning between the photosynthetic apparatus and cell wall proteins.

#### Leaf senescence and shedding

Leopold (1961) categorized leaf senescence into four types: (1) ‘over-all senescence’ in monocarpic species, in which the entire individual dies in an abrupt manner; (2) ‘top senescence’ in perennial herbs, in which the whole above-ground part dies; (3) ‘deciduous senescence’ in deciduous woody species, in which only leaves dies; and (4) ‘progressive senescence’ in the growing season when younger leaves are still active. The first three types are strategies to avoid stress in a non-favourable season. In the following the progressive senescence is discussed.

The progressive senescence has been studied intensively for herbaceous species. In many herbaceous plants photosynthetic capacity and nitrogen content of a leaf are highest at its full expansion and thereafter decline linearly with time (Thomas and Stoddart, 1980; Smart, 1994). Parallel changes in photosynthetic capacity and nitrogen content are caused by the photosynthetic proteins that are degraded through senescence with a constant specific activity (Makino *et al.*, 1983). Degraded nitrogenous compounds, mainly

amino acids, are translocated to other organs, leading to reduction in the leaf nitrogen content (Makino *et al.*, 1983; Hidema *et al.*, 1991; Hikosaka, 1996). Thus it is widely accepted that leaf senescence is accompanied by recycling of nitrogen within a plant (Thomas and Stoddart, 1980; Smart, 1994).

Plants alter the rate of leaf senescence depending on growth environment. Light is one of factors responsible for regulation of leaf senescence. According to the theory of nitrogen allocation among leaves, retranslocation of nitrogen from shaded to sunlit leaves will increase photosynthetic gain of the whole plant. Several studies have tested the hypothesis that shading a leaf accelerates retranslocation of nitrogen from the leaf. Hirose *et al.* (1988) established stands of *Lysimachia vulgaris*, a perennial herb, with different plant densities and found that the vertical gradient of leaf nitrogen content was steeper in the dense stand, suggesting that mutual shading accelerated retranslocation of nitrogen. Several experiments in which parts of leaves were artificially shaded showed that nitrogen is retranslocated from shaded to unshaded leaves (Evans, 1989b; Hikosaka *et al.*, 1994; Pons and Percy, 1994; Ackerly and Bazzaz, 1995).

The effect of shading is not simple because shading of the whole plant delays leaf senescence (Hidema *et al.*, 1991; Ono *et al.*, 1996; Terashima *et al.*, 2005), which seems to contradict the studies above. Hikosaka (1996) suggested that leaf senescence due to shading is affected by the manner of shading, i.e. whether part or all of leaves are shaded. Different nitrogen demand in sink organs influences the pattern of leaf senescence. Retranslocation of nitrogen from old leaves is affected not only by physiological status of the leaf but also by development of sink organs; when plants are growing fast, much nitrogen is required for construction of new tissues, which accelerates senescence in old leaves (Nambias and Fife, 1987; Ono *et al.*, 1996). When all leaves of the plant are shaded, plant growth is limited by light. Retranslocation of nitrogen from older leaves may be slow owing to low sink activities. When part of leaves of a plant is shaded with the other leaves receiving strong light, higher plant growth rates are maintained by photosynthesis of the latter. In this case, nitrogen retranslocation is accelerated with great demand of nitrogen in developing organs (Fig. 1).

This idea may be supported by several branch-level studies. Stoll and Schmid (1998) determined branch growth of trees at the edge and at the centre of a tree patch. Branch growth was greatest in sun branches and, interestingly, shade branches of the trees at the edge had lower growth rates than shade branches of the trees at the centre, though the former received higher PFDs. Thus branch growth was not a simple function of PFD. Takenaka (2000) studied the relationship between the mortality rate and PFD in branches of plants growing at different PFDs. When compared among branches that receive similar PFDs, the mortality rate of the branch was higher in plants growing at higher PFDs. These results have been interpreted as an optimal foraging strategy; plants may allocate more resources to branches in favourable conditions at the expense of growth and survivorship of branches in unfavourable conditions.

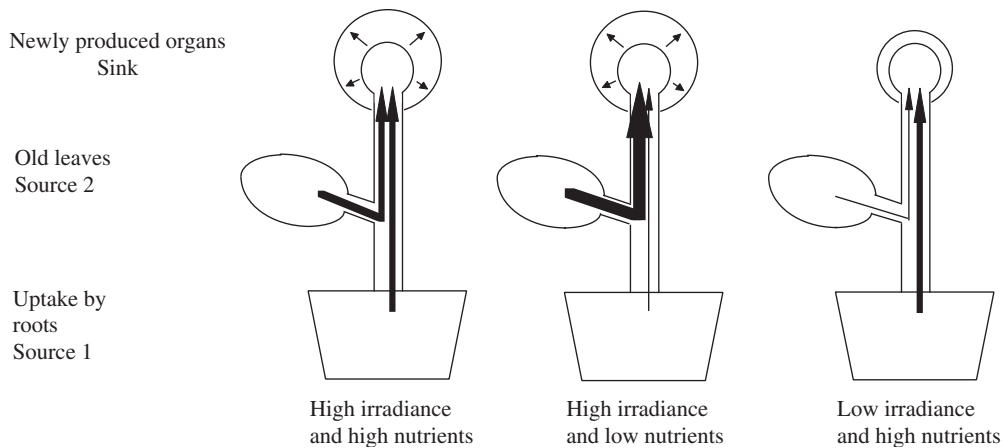


FIG. 1. Sink and source relationship for nitrogen in plants. Developing organs require nitrogen, which is supplied either from nitrogen uptake in roots (source 1) or retranslocation from old leaves (source 2). When the plant is growing at high irradiance and high nutrient availability, nitrogen is supplied from the two sources. Retranslocation from old leaves is accelerated when nutrient supply is limited, and lowered when irradiance is low.

Nitrogen deficiency is known to accelerate leaf senescence (Thomas and Stoddart, 1980; Makino *et al.*, 1983, 1984; Guitman *et al.*, 1991; Smart, 1994). This is also related to nitrogen demand in sink organs. For production of new tissues, plants have two sources of nitrogen. One is uptake by roots and the other is retranslocation from old organs (Fig. 1). If rates of nitrogen uptake in roots are low, sink organs may accelerate senescence in old leaves to satisfy their nitrogen demand. Ono *et al.* (1996) showed that nitrogen deficiency in new organs varies with sink development and nitrogen uptake rates, and that the rate of leaf senescence is well correlated with nitrogen deficiency.

Several ecological studies have shown that the leaf lifespan is longer in plants growing under lower nutrient availability (see Aerts and Chapin, 2000), which seems to contradict the results from physiological studies. This may be explained by different regimes of nitrogen deficiency (Hikosaka, 2003). Ecologists usually use field plants where nitrogen turnover is nearly at a steady state, while physiological experiments often subject plants to a sudden change in nitrogen supply. Plants growing under chronic nitrogen deficiencies have a lower productivity, which leads to a smaller demand for nitrogen in sink organs. On the other hand, when plants that have been under high nitrogen availability are subjected to a sudden reduction in nitrogen supply, nitrogen becomes deficient in the growing organs. This will accelerate nitrogen translocation from old organs. Mutual shading may also be responsible for the different results between ecological and physiological studies in relation to response to nutrient deficiency. In plants under chronic nitrogen deficiency LAI is small (Aerts and de Caluwe, 1994a; Anten *et al.*, 1995b), which lowers mutual shading and may thus retard leaf senescence.

Leaf ageing has a significant effect on photosynthesis even when environmental factors do not change. Hikosaka *et al.* (1994) studied leaf senescence in the vine *Ipomoea tricolor* grown horizontally to avoid mutual shading. When

all leaves were exposed to full sunlight, allocation of leaf nitrogen was affected by nutrient availability. At a lower nitrogen availability nitrogen was retranslocated from old to new leaves, leading to a steeper gradient of leaf nitrogen content, while at a high nitrogen availability the oldest leaves kept a high nitrogen content, which was comparable to that of new leaves. High nitrogen content in old leaves did not mean a high photosynthetic capacity in this case. Hikosaka (1996) determined nitrogen allocation within leaves of *I. tricolor*. Old leaves in plants with high nitrogen availability without any shading maintained a high nitrogen content but had smaller amounts of photosynthetic proteins such as ribulose-1,5-bisphosphate carboxylase, cytochrome *f* and photosystems, leading to low photosynthetic capacities. This result suggests that photosynthetic capacity is not necessarily coupled with nitrogen content.

Patterns of leaf senescence in evergreen woody species are not the same as those in herbaceous species. First, in the temperate region, changes in leaf nitrogen contents are not simply age-dependent but affected by the seasonal environment. For example, in the understorey of deciduous forests, light availability is high and air temperature is low in winter. These environmental factors induce an increase in the leaf nitrogen content. Thus the leaf nitrogen content and photosynthetic capacity of evergreen understorey species show large fluctuations within a year (Kume and Ino, 1993; Skillman *et al.*, 1996). Secondly, in evergreen trees with a longer leaf lifespan, decrease in photosynthetic capacity is not necessarily coupled with that in leaf nitrogen content. A parallel decline in photosynthetic capacity and leaf nitrogen content has been observed in some species (Field and Mooney, 1983; Kitajima *et al.*, 1997), while there are also reports that photosynthetic capacity gradually decreases while nitrogen content remains relatively constant until the end of the life of a leaf (Kitajima *et al.*, 2002, 2005; Escudero and Mediavilla, 2003). Causes of the decrease in photosynthetic capacity in such species have not been clarified.

There may be two factors regulating photosynthetic capacity; one is the age-dependent decrease in photosynthetic capacity and the other is the protein degradation controlled by the sink–source relationship (Fig. 1). In fast-growing plants, leaf senescence is almost always coupled with nitrogen re-allocation because the high growth rate accelerates retranslocation of nitrogen from an old leaf, which may occur faster than the age-dependent reduction in photosynthetic capacity of the leaf. Whether it is also the case for species with a long leaf lifespan is questionable, but Kikuzawa (2003) reported that photosynthetic capacity declined with time in a shoot of *Fagus crenata*, a flush-type deciduous tree, although the light environment did not change much throughout year.

#### *Nitrogen resorption*

When leaves senesce, some nitrogen in the leaf is resorbed while the other remaining in the leaf is lost from plants with shedding. This is also the case in species that maintain a high leaf nitrogen content until the end of the life of a leaf (Escudero and Mediavilla, 2003). Since nitrogen is a limiting element in most plants, recycling of nitrogen is beneficial. May and Killingbeck (1992) showed that plant growth is suppressed when nitrogen resorption is prevented. The nitrogen resorption efficiency is defined as the fraction of nitrogen resorbed from living leaves (Aerts and Chapin, 2000). The larger the nitrogen resorption efficiency is, the more nitrogen is reutilized by the plant. There has been much discussion on the factors that determine the nitrogen resorption efficiency. Some suggested that plants in lower nutrient availabilities have a higher nitrogen resorption efficiency (Boerner, 1984; Shaver and Melillo, 1984; Aerts and de Caluwe, 1994b), while many others did not find such relationships (Schlesinger *et al.*, 1989; Chapin and Moilanen, 1991; Escudero *et al.*, 1992a). From a literature survey, Aerts (1996) concluded that there is no consistent trend in nitrogen resorption efficiency against nitrogen availabilities.

Killingbeck (1996) argued that nitrogen resorption is determined by its end-point rather than the fraction of resorption. He defined the nitrogen resorption proficiency, which is the nitrogen concentration on a mass- or an area-basis of dead leaves. From the survey of various studies, he suggested that 0.7 % (mass-basis) or 0.5 g m<sup>-2</sup> (area-basis) is the end-point and that plants with the nitrogen content in dead leaves higher than these values may indicate incomplete nitrogen resorption.

Several studies have argued that there is a certain amount of nitrogen that cannot be retranslocated (non-labile nitrogen), which is derived from the *X*-intercept in the linear regression of photosynthetic capacity and nitrogen content (Charles-Edwards *et al.*, 1987; Anten *et al.*, 1995a). This idea is supported by the fact that the same photosynthesis–nitrogen relationship holds across growth conditions and leaf ageing within a species. However, it is still uncertain whether the *X*-intercept actually represents non-labile nitrogen. Recently, Yasumura *et al.* (2004) showed, in three deciduous tree species, that the nitrogen content in dead leaves was higher than the *X*-intercept values.

## LEAF TURNOVER AS A STRATEGY

### *Carbon balance, nitrogen use and leaf lifespan*

Leaf lifespan, an inverse of the turnover rate of leaves, varies among species by two orders of magnitude (Reich *et al.*, 1992). A longer leaf lifespan tends to be found more in woody than in herbaceous species (Reich, 1993), in species living in habitats with poor nutrient availability (Aerts and Chapin, 2000), and in slow-growing species (Reich *et al.*, 1992). Now it is widely accepted that there is a convergence of leaf traits; species with a longer leaf lifespan have a lower photosynthetic capacity per unit mass, a lower photosynthetic capacity per unit area, a lower nitrogen concentration per unit mass, and a higher LMA irrespective of life form, phylogeny and biomes (Reich *et al.*, 1997, 1999; Wright *et al.*, 2004), though the relationship slightly shifts depending on habitats (Reich *et al.*, 1999; Wright *et al.*, 2001, 2004). Within a species, leaf lifespan varies with growth environment. Many studies have shown that low growth irradiance extends leaf lifespan (Chabot and Hicks, 1982; Kikuzawa, 1988; Williams *et al.*, 1989; Osada *et al.*, 2001, 2003; Fig. 2).

In 1980s, several authors incorporated a cost–benefit theory to analyse the variation in leaf lifespan (Chabot and Hicks, 1982; Mooney and Gulmon, 1982). A leaf needs to acquire a certain amount of carbon, at least, to construct one new leaf to maintain the number of leaves in the canopy. Thus leaves with lower rates of photosynthesis should have a longer lifespan to pay back the construction cost. Williams *et al.* (1989) determined photosynthesis, leaf construction cost, and leaf lifespan of seven *Piper* species in different light environments in a tropical rain forest. They found that the ratio of the construction cost to daily photosynthesis, which they called ‘payback time’, was positively correlated with actual leaf lifespan. Similar correlations have been observed in other studies (Sobrado, 1991; Emaus and Prichard, 1998; Navas *et al.*, 2003; Oikawa *et al.*, 2004). These results support the cost–benefit hypothesis.

Several authors noticed that the rate of photosynthesis per unit mass scales the  $-2/3$  power of leaf longevity in the broad interspecific comparison conducted by Reich *et al.* (1999) (Westoby *et al.*, 2000; Givnish, 2002). This implies that, if no reduction in leaf photosynthesis is assumed, a leaf with a longer lifespan has a greater life-time carbon gain that is the product of the rate and duration of photosynthesis. Givnish (2002) suggested that species with a longer leaf lifespan may need greater carbon gain than expected when one focuses on leaf performance only, because they invest more biomass in roots to survive in low-productive, highly infertile or dry habitats. Westoby *et al.* (2000) considered the effect of time discounting on the value of captured light or photosynthesis. Persistence of leaves for a longer period is disadvantageous due to overshadowing by surrounding vegetation or due to risk of damage such as herbivory. Furthermore, earlier carbon gain in a leaf may be more valuable because it can be reinvested in new leaves, resulting in a greater compound-interest (the opportunity–cost effect; for detail see also Harper, 1989). However, field studies have suggested that life-time carbon gain is not very different between leaves with different longevity (Chabot

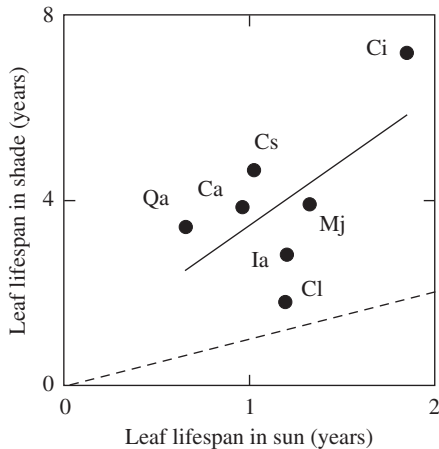


FIG. 2. Leaf lifespan of evergreen species at a forest edge (sun) and understorey (shade) Cs, *Castanopsis sieboldii*; Qa, *Quercus acuta*; Ca, *Camellia japonica*; Cl, *Cleyera japonica*; Ci, *Cinnamomum japonicum*; Ia, *Illicium anisatum*; Mj, *Maesa japonica*. Continuous and dotted line denote regression and 1 : 1 line, respectively (K. Hikosaka, unpubl. res.). For description of the site, see Hikosaka and Hirose (2000).

and Hicks, 1982; Diemer and Körner, 1996; Mediavilla and Escudero, 2003). Comparing Mediterranean evergreen species, Mediavilla and Escudero (2003) showed that the effect of the reduction in the photosynthetic capacity on life-time carbon gain was greater in species with a longer lifespan. Thus the time-discounting effect may mainly be ascribed to leaf senescence.

Leaf lifespan has been discussed in relation to nitrogen use in leaves. Small (1972) showed that deciduous species have a higher rate of photosynthesis, while evergreen species utilize nitrogen for a longer period. This idea was extended to a plant-level nitrogen use efficiency (NUE), defined as the biomass production per unit nitrogen taken up. NUE has been expressed as the product of nitrogen productivity (NP; biomass production per unit nitrogen in the plant body) and mean residence time of nitrogen (MRT) (Berendse and Aerts, 1987). MRT is a positive function of leaf lifespan (Escudero *et al.*, 1992b; Aerts and Chapin, 2000). It was shown that deciduous species have a higher NP, whereas evergreen species have a longer MRT (Berendse and Aerts, 1987; Aerts, 1990; Eckstein and Karlsson, 1997), leading to a similar NUE between species.

Why are there no species that have both high productivity (photosynthetic capacity or NP) and long persistence (leaf lifespan or MRT)? One of important reasons may be structural and physiological constraints (Reich *et al.*, 1991). As mentioned above, leaves with a high photosynthetic capacity have a lower leaf toughness (Reich *et al.*, 1991; Wright and Westoby, 2002). Having higher photosynthetic capacity or PNUE may require a considerable investment of nitrogen in the photosynthetic apparatus at the expense of the investment in cell wall proteins (Onoda *et al.*, 2004; Takashima *et al.*, 2004). A leaf may not satisfy both at the same time. On the other hand, species with a low productivity and short persistence may have been eliminated by natural selection (Reich *et al.*, 1991).

Such physiological constraints, however, do not necessarily explain all the variations in leaf lifespans. For example, as mentioned above, sun leaves have a shorter lifespan than shade leaves, although sun leaves may have a greater leaf toughness due to higher LMA. If sun leaves had a leaf lifespan that was comparable to that of shade leaves, they would realize the highest carbon gain. Why do sun leaves fall earlier than shade leaves? Optimality models are useful for comprehensive understanding of leaf lifespan.

#### Optimality models of leaf turnover

Kikuzawa (1991) extended the cost–benefit theory to a simple optimality model of leaf lifespan. He assumed (a) that construction cost of a leaf ( $C$ ) is incurred at leaf birth, (b) that rate of photosynthesis of a leaf decreases linearly with time, (c) that the number of leaves in the canopy is constant, and (d) leaf lifespan is regulated to maximize carbon gain at the canopy level, not at the leaf level. Then he derived the optimal leaf lifespan ( $L_{opt}$ ):

$$L_{opt} = (2bC/a)^{0.5} \quad (2)$$

where  $a$  is the maximum rate of photosynthesis of a leaf at leaf birth,  $b$  the time when the rate of photosynthesis becomes zero (potential leaf longevity) and  $C$  the construction cost of a leaf.  $a/b$  indicates the rate of decline in the rate of photosynthesis. The model predicts that a leaf is shed when the net gain by a leaf per unit time over the entire lifespan becomes maximal even when the leaf could continue to photosynthesize. Although production of a new leaf requires an investment of biomass, the replacement improves the carbon gain of the canopy instead of maintaining old, less productive leaves. This model explains variation in leaf lifespan; it predicts that plants will have a shorter leaf lifespan if leaves have higher rates of photosynthesis, a higher rate of decline in rate of photosynthesis or smaller construction cost. Kikuzawa and Ackerly (1999) have shown that the calculated  $L_{opt}$  for actual plants was strongly correlated with the observed leaf lifespan.

The model of Kikuzawa (1991) is not sufficient to explain the behaviour of the leaf canopy because it does not predict the total number of leaves in the canopy. As discussed above, photosynthetic traits of a leaf are strongly influenced by shading in the canopy, suggesting that leaf senescence is dependent on position rather than age (Ackerly, 1999). Ackerly (1996) showed that if a steady state is assumed for turnover of leaves, leaf lifespan ( $L_n$ ) is expressed by:

$$L_n = N/r \quad (3)$$

where  $N$  is the number of leaves and  $r$  is the leaf birth rate (the number of leaves produced per unit time). If we use LAI and the rate of leaf production instead of  $N$  and  $r$ , respectively, lifespan at a canopy level ( $L_a$ ) in terms of leaf area can be expressed as

$$L_a = F_{can}/G_{can} \quad (4)$$

where  $F_{can}$  is the leaf area index (LAI) and  $G_{can}$  is the rate of leaf area production (see eqn 1).  $L_n$  is equal to  $L_a$  if the area of a leaf is constant. Ackerly (1999) proposed an alternative

optimality model in which the leaf birth rate is maximized. In a competing system, height growth is important to outcompete neighbours (Weiner, 1990; Nagashima and Terashima, 1995). The height growth of plants depends on the addition and elongation of internodes, and each internode is produced in association with a new leaf (Ackerly, 1999). Ackerly (1999) assumed that the rate of photosynthesis is position-dependent, in which the number of younger leaves determines the rate of photosynthesis of older leaves, and derived the optimal solution to maximize the leaf birth rate ( $L_r$ ):

$$L_r = 2C/(aA_L) \quad (5)$$

where  $A_L$  is biomass allocation to leaves (see eqn 1). In this optimal solution, the oldest leaf drops when its photosynthesis becomes zero.

Kikuzawa's model assumes that assimilated carbon minus carbon invested for leaf construction (i.e. revenue minus cost) per unit time is maximized, while Ackerly's solution maximizes the leaf production rate, which is proportional to the amount of carbon invested for leaf construction. Thus the two solutions are different from each other. Ackerly (1999) compared the leaf turnover predicted by his model and Kikuzawa's with observation of pioneer species in a tropical forest. Observed values were correlated with prediction by both models, but the difference between observed and predicted values was smaller in the model of Ackerly (1999).

Recently, Escudero and Mediavilla (2003) presented a new hypothesis to explain leaf lifespan. In Mediterranean evergreen species, the photosynthetic capacity of leaves decreased with leaf ageing. Since the leaf nitrogen content does not decrease until the end of the life of a leaf, the decrease in photosynthetic capacity was ascribed to a reduction in PNUE. Photosynthetic gain in a plant is maximized by shedding older leaves only when photosynthesis by retranslocated nitrogen in new leaves exceeds the photosynthesis of the leaves lost (Franklin and Ågren, 2002). This condition is satisfied when the ratio of PNUE in the old leaves to PNUE in the young leaves becomes lower than the nitrogen resorption efficiency. Escudero and Mediavilla (2003) showed that, in the nine species that they studied, the ratio of PNUE in the oldest leaves to PNUE in the youngest leaves was similar or lower than the nitrogen resorption efficiency, which is consistent with their hypothesis.

To extend the hypothesis of Escudero and Mediavilla (2003) to an optimality model, however, turnover of nitrogen needs to be incorporated. Since plants lose nitrogen with dead leaves, plants should drop leaves after they take up nitrogen in an amount large enough to compensate for the lost nitrogen. Otherwise the amount of nitrogen in the canopy would decrease. Thus the optimal leaf lifespan may be a function of two factors: the rate of nitrogen uptake and of PNUE reduction.

#### *Leaf turnover and canopy photosynthesis*

The canopy photosynthesis model has been used to analyse canopy structure and function (Monsi and Saeki, 1953;

see Hirose, 2005). In previous studies the canopy has been treated as a static system and dynamic aspects have been paid less attention. However, the canopy photosynthesis model may also be useful for the analysis of canopy dynamics such as leaf lifespan. Leaf production is determined by the rate of photosynthesis of the canopy (eqn 1) and leaf shedding is a removal of excessive leaves that do not contribute to canopy photosynthesis. Hikosaka (2003) incorporated dynamics of leaves and nitrogen into a canopy photosynthesis model. Figure 3 outlines the structure of the model. Leaf area in the canopy increases with the production of new leaves, which is proportional to the rate of photosynthesis in the canopy (eqn 1). Uptake of nitrogen from the soil increases the amount of nitrogen in the canopy. The optimal LAI that maximizes canopy photosynthesis is calculated. If leaf area is in excess, old leaves are eliminated, and part of nitrogen is lost with dead leaves. Consequently a new canopy having an optimal LAI with an optimal amount of nitrogen is obtained. Repeating this process gives growth of the leaf canopy.

One of the important assumptions in the model of Hikosaka (2003) is the optimization of LAI. Earlier models for canopy photosynthesis have predicted that the canopy should increase LAI until PFD at the bottom of canopy equals the compensation point of daily photosynthesis (e.g. Saeki, 1960; Verhagen *et al.*, 1963). However, LAI is determined not only by light, but also by nutrient availability (Aerts and de Caluwe, 1994a; Ackerly and Bazzaz, 1995; Anten *et al.*, 1995b). When the amount of nitrogen in the canopy is limited, mean nitrogen content per unit leaf area decreases with increasing LAI, resulting in low canopy photosynthesis. Anten *et al.* (1995b) calculated the effect of LAI on the rate of photosynthesis in the canopy with the amount of nitrogen in the canopy being kept constant, where nitrogen distributes optimally among leaves. They found an optimal LAI that maximizes canopy photosynthesis for a given canopy nitrogen, which showed a strong correlation with observed LAI. Their theory has been incorporated in the model of Hikosaka (2003).

The amount of nitrogen lost with dead leaves has two important effects on leaf turnover. First, it affects optimal LAI (Franklin and Ågren, 2002). Consider a canopy having a LAI that is higher than the optimal LAI at a given canopy nitrogen. Some leaves may be in excess, but leaf shedding decreases canopy nitrogen content as dead leaves contain some nitrogen. The canopy should shed leaves only when shedding increases canopy photosynthesis. Franklin and Ågren (2002) showed that the canopy that has smaller nitrogen resorption efficiency should have a higher LAI.

The second, more important effect is that the nitrogen concentration in dead leaves determines the rate of leaf turnover (Hikosaka, 2003). A leaf canopy absorbs carbon and nitrogen to produce leaves and loses them with dead leaves. When leaf turnover is at a steady state, by definition, the rate of leaf mass production is equal to the rate of leaf mass loss, and the rate of nitrogen uptake in leaves is equal to the rate of nitrogen loss. Nitrogen concentration of dead leaves is, also by definition, equal to the ratio of the loss rate of nitrogen to the loss rate of leaf mass (Vitousek, 1982; Yasumura *et al.*, 2002). Thus the rate of leaf mass

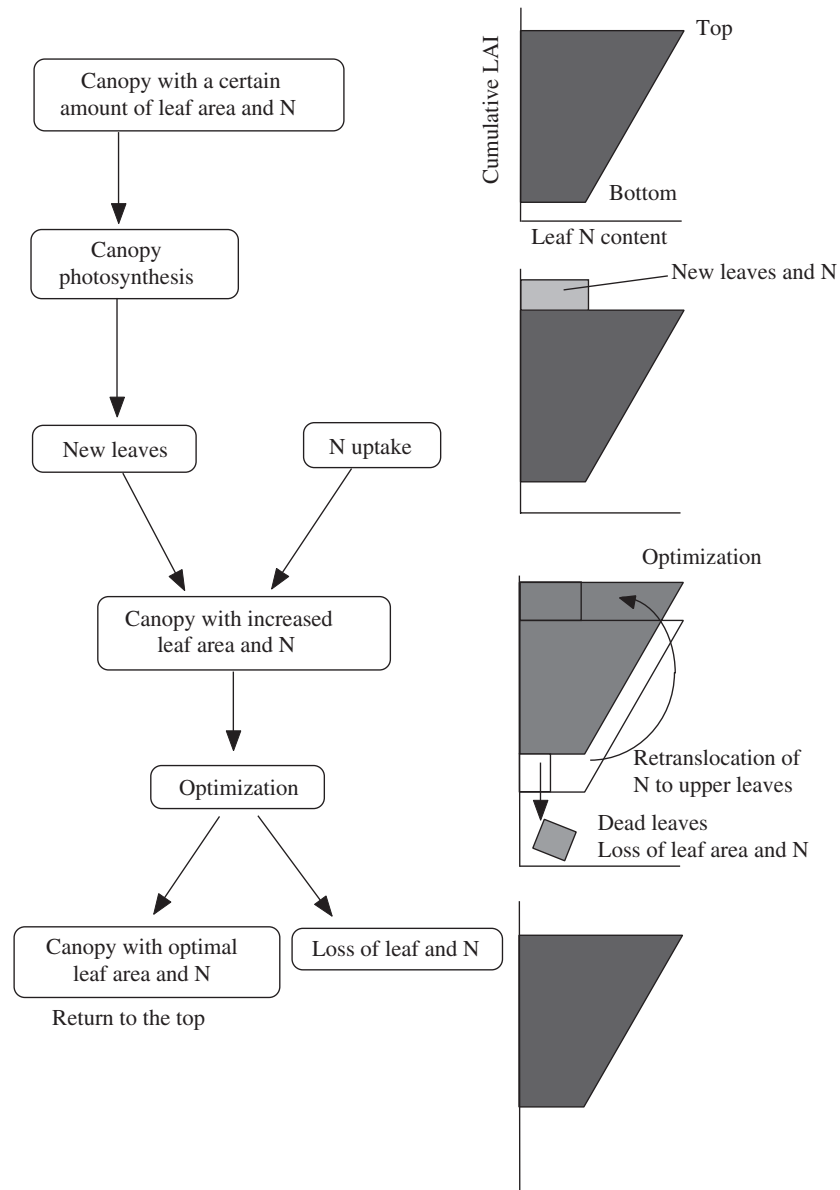


FIG. 3. A schematic diagram of the leaf turnover model of Hikosaka (2003). See text for details.

production is given as the ratio of the nitrogen uptake rate to the nitrogen concentration of dead leaves. Even if the canopy has a potential of higher canopy photosynthesis, the rate of photosynthesis in the canopy is regulated so as to meet the nitrogen uptake rate. Lower nitrogen concentrations in dead leaves may be advantageous at low nutrient availability because it allows a high canopy photosynthetic capacity at a given nitrogen uptake rate.

When a factor other than nitrogen (such as light) limits canopy photosynthesis, low nitrogen concentrations in dead leaves may be disadvantageous. If the ratio of the nitrogen uptake rate to leaf mass production is higher than the nitrogen concentration of dead leaves, nitrogen continues to accumulate in the leaf canopy, which would lead to excessively high nitrogen contents in leaves. Excessive nitrogen, increasing respiration, would not increase carbon gain and

may only attract herbivores. When nutrient availability is relatively high, plants need to decrease nitrogen uptake rates or to increase nitrogen concentration of dead leaves to avoid excessive accumulation of nitrogen. A canopy with low nitrogen concentrations in dead leaves would not be favoured at high nitrogen availabilities. Supraoptimal nitrogen contents of living leaves are often observed in sun species that are growing in extremely low light conditions (Anten and Werger, 1996; Hikosaka and Terashima, 1996; Anten *et al.*, 1998; Hikosaka *et al.*, 1999). Such plants sometimes shed green leaves that contain a considerable amount of nitrogen (Y. Yasumura, pers. comm.). Plants balance the flux of nitrogen and carbon in the canopy.

These results suggest that nitrogen loss from the canopy plays an important role in leaf dynamics. It should be noted that the leaf turnover rate depends more strongly on nitrogen



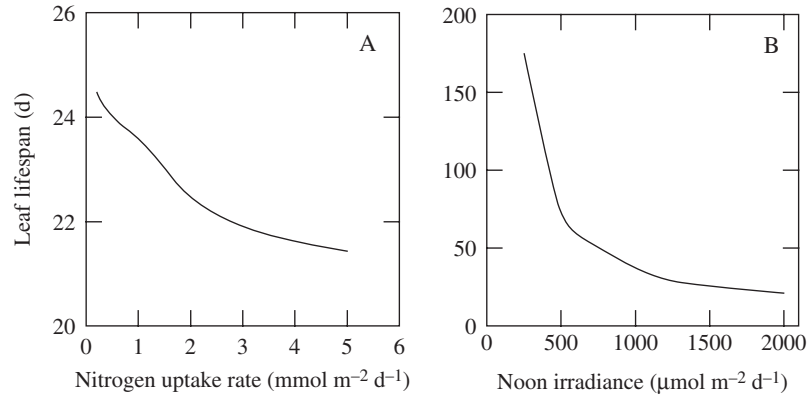


FIG. 4. (A) Predicted leaf lifespan as a function of nitrogen uptake rate (a measure of nitrogen availability) and (B) noon irradiance (a measure of light availability). Noon irradiance is assumed to be  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  in (A) and nitrogen uptake rate is assumed to be maximal in (B) (the maximal nitrogen uptake rate is the upper limit where the leaf turnover is maintained at a steady state and increases with noon irradiance). Redrawn from Hikosaka (2003).

concentration of dead leaves than on nitrogen concentration of living leaves or on nitrogen resorption. Thus the nitrogen resorption proficiency (Killingbeck, 1996) can be the most important parameter to determine leaf dynamics.

The model of Hikosaka (2003) incorporated several physiological processes to evaluate environmental responses of canopy structure and leaf turnover.

- Nitrogen availability. Higher nitrogen availability leads to the greater LAI. This is because higher nitrogen uptake rates allow higher rates of photosynthesis in the canopy. Leaf lifespan is predicted to be slightly longer at lower nitrogen availabilities (Fig. 4A), which is due partly to lower rates of canopy photosynthesis (see eqn 3). This result is consistent with previous studies that showed shorter leaf lifespan at higher nutrient availability (see Aerts and Chapin, 2000).
- Light availability. Leaf lifespan is longer at low irradiance (Fig. 4B), which also results from the low rate of canopy photosynthesis. This is consistent with previous studies (Chabot and Hicks, 1982; Kikuzawa, 1988; Osada *et al.*, 2001).
- PNUE or elevated  $\text{CO}_2$ . Effects of the slope of the photosynthesis–nitrogen relationship are shown in Fig. 5. Interestingly, increase in the slope increases neither the rate of photosynthesis in the canopy nor the LAI at a steady-state leaf turnover. This is because the rate of photosynthesis in the canopy is always proportional to the ratio of nitrogen uptake rate to nitrogen concentration in dead leaves irrespective of other factors. As the slope of the photosynthesis–nitrogen relationship increases, the mean nitrogen content per unit leaf area in the canopy decreases in a counteracting manner (Fig. 5). This may explain the long-term response to elevated  $\text{CO}_2$  ( $\text{CO}_2$  acclimation); elevated  $\text{CO}_2$  increases the slope of the photosynthesis–nitrogen relationship but long-term growth at elevated  $\text{CO}_2$  often reduces the leaf nitrogen content such that the *in situ* rate of photosynthesis in the leaf is similar to that in leaves growing at normal  $\text{CO}_2$  (Sage, 1994; Makino and Mae, 1999).

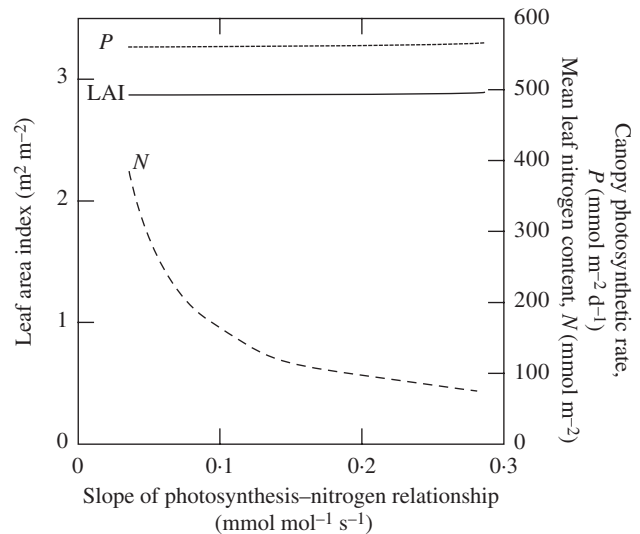


FIG. 5. Influence of the slope of the photosynthesis–nitrogen relationship on canopy characteristics. Noon irradiance and nitrogen uptake rate are  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $4 \text{mmol m}^{-2} \text{d}^{-1}$ , respectively. Redrawn from Hikosaka (2003).

- LMA. The model predicts that an increase in LMA extends leaf lifespan because it decreases the rate of leaf area production (see eqn 1). This is consistent with field observations (e.g. Reich *et al.*, 1992).

#### Leaf turnover and evolutionary game

The optimal strategy that maximizes photosynthesis of the whole canopy would not be evolutionarily stable when the revenue of an individual is affected by neighbours' strategy (Givnish, 1982; Maynard-Smith, 1982). In plant canopies, especially in herbaceous canopies, individual plants compete for light with their neighbours and light interception of an individual is strongly affected by neighbours (Hikosaka *et al.*, 2001). Hikosaka and Hirose (1997) incorporated the game theory into a canopy photosynthesis model and examined evolutionarily stable leaf angle. The

photosynthetic capacity of canopies with vertical leaves exceeds those with horizontal leaves, because more light passes through to reach deeper layers, resulting in more uniform distribution of light within the canopy as mentioned above. However, horizontal leaves intercept light more than vertical leaves under the same light intensity. If a mutant with horizontal leaves appears in a stand of individuals with vertical leaves, photosynthesis of the mutant would exceed that of neighbours because of its greater light interception. Therefore, the evolutionarily stable leaf angle is expected to be more horizontal than the 'optimal' leaf angle that maximizes whole canopy photosynthesis. Similar logic has been applied to the evolutionarily stable LAI. The evolutionarily stable LAI is shown to be greater than the optimal LAI (Schieving and Poorter, 1999; Anten, 2002; see Anten, 2005).

No one seems to have discussed the evolutionarily stable leaf turnover rate. The pattern of leaf turnover that maximizes the leaf birth rate (Ackerly, 1999) may be closer to the evolutionarily stable strategy because, as mentioned above, height growth is important to compete with neighbours. If the evolutionarily stable canopy has a greater LAI than the optimal canopy, the former has a lower rate of photosynthesis than the optimal canopy (Hikosaka and Hirose, 1997; Anten, 2002). Then it will extend the leaf lifespan of the plant (see eqn 3).

## CONCLUSIONS

Leaf dynamics are affected by various environmental and internal factors, where nitrogen plays an important role. The effects of nitrogen can be summarized as follows. (a) Nitrogen is a determinant of the rate of photosynthesis. Its amount in the canopy and its allocation among leaves have large effects on canopy photosynthesis. (b) Nitrogen is utilized efficiently by retranslocation from old leaves. Old leaves are an alternative source of nitrogen for sink organs when nitrogen uptake of roots does not meet sink demand. If sink organs require more nitrogen, senescence of old leaves is accelerated. (c) When leaf turnover is at a steady state, the ratio of biomass production to nitrogen uptake (i.e. NUE) is equal to the ratio of litter fall to nitrogen loss, which is an inverse of the nitrogen concentration in dead leaves. Thus nitrogen concentration in dead leaves (nitrogen resorption proficiency) and nitrogen availability in the soil determine the rate of photosynthesis in the canopy. Leaf turnover is an important process leading to maximization of carbon gain and resource-use efficiency. It may also affect success in competition with neighbours. The optimality and the game theory may be useful tools to analyse and to predict environmental response of canopy characteristics.

## ACKNOWLEDGEMENTS

I thank T. Hirose, S. Oikawa and Y. Yasumura for comments. This study was supported in part by grants from the Japanese Ministry of Education, Science, Sports, and Culture.

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