Plant growth based on interrelation between carbon and nitrogen translocation from leaves

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Abstract

In individual leaves, the photon-saturated photosynthetic activity (P_{sat}, expressed on a dry mass basis) was closely related to the nitrogen content (Nc) as follows: $P_{sat} = \text{Cf Nc} + P_{sat0}$, where Cf and P_{sat0} are constants. On a whole plant basis, the relative growth rate (RGR) was closely related to Nc in canopy leaf as follows: $\text{RGR} = \text{DMf Nc} + \text{RGR}_0$, where DMf and RGR_0 are constants. However, the coefficients Cf and DMf were markedly different among plant species. To explain these differences, it is suggested that carbon assimilation (or dry matter production) is controlled by both the Nc in a leaf (or leaves) and by the net N translocation from leaves. This is supported by the finding that P_{sat} is related to the rate of ^{35}S-methionine translocation from leaves. We propose another estimation method for the net N translocation rate (NFR) from leaves: Nc, after full leafing, is expressed as a function of time: $\text{Nc} = (\text{Nc}_0 - \text{Ncd}) \exp(-\text{Nf}\, t) + \text{Ncd}$, where Nf is a coefficient, t is the number of days after leaf emergence, Nc_0 is the initial value of Nc, and Ncd is the Nc of the dead leaf. The NFR is then calculated as $\text{NFR} = \Delta\text{Nc}/\Delta t = -\text{Nf}\,(\text{Nc} - \text{Ncd})$. Thus Nf is the coefficient for the NFR per unit Nc. NFR is a good indicator of net N translocation from leaves because NFR is closely related to the rate of ^{35}S-methionine translocation from leaves. Since P_{sat} is related to the ^{14}C-photosynthate translocation rate, Cf (or DMf) corresponds to the coefficient of saccharide translocation rate per unit amount of Nc. Cf (or DMf) is closely related to the Nf of individual leaves (or the Nf of canopy leaf). This indicates that C assimilation and C translocation from leaves are related to Nc and N translocation from leaves (net translocation of N). Cf and Nf are negatively correlated with leaf longevity, which is important because a high or low CO_2 assimilation rate in leaves is accompanied by a correspondingly high or low N translocation in leaf, and the degree of N translocation in leaves decreases or increases leaf longevity. Thus, since a relatively high P_{sat} (or RGR) is accompanied by a rapid Nc decrease in leaves, it is difficult to maintain a high P_{sat} (or RGR) for a sustained time period.

Additional key words: ^{14}C-photosynthate; canopy; leaf longevity; photosynthesis; relative growth rate; ^{35}S-methionine; senescence.

Introduction

There is a positive correlation between the leaf nitrogen content (Nc) and photon-saturated leaf photosynthetic rate (P_{sat}) (Gulmon and Chu 1981, Field and Mooney 1986, Hirose and Kitajima 1986, Evans 1989). The P_{sat}-Nc relation varies with the growth stages (Murata 1961, Hayami 1982) or plant species (Evans and Seemann 1989). In the analysis of ontogenetic changes of P_{sat} among several crops, when P_{sat} and Nc were expressed on a dry mass basis, P_{sat} showed a close positive relationship with Nc regardless of leaf position or growing conditions over a long growth period (Osaki *et al.* 2001). However, the P_{sat}-Nc regression coefficient was different among field crops, which could not be explained by the leaf structure (leaf mass per area, LMA) or concentration of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) (Osaki *et al.* 2001). Ingestad (1977, 1979) found a linear relationship between RGR and Nc of the whole plant in trees. Greenwood *et al.* (1991) reported that in field crops RGR was not linearly related to Nc of whole plant, and that the modified RGR was used to

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Abbreviations: Cf, coefficient of net carbon translocation rate of leaf; CFR, net carbon translocation rate from leaf; DMf, coefficient of net carbon translocation rate of whole plant; LMA, leaf mass per area; Nc, nitrogen content; Nf, coefficient of net nitrogen translocation rate; NFR, net nitrogen translocation rate from leaf; P_{sat}, net photosynthetic rate saturated with photons; RGR, relative growth rate; RuBPCO, ribulose 1,5-bisphosphate carboxylase/oxygenase.

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adapt the linear relationship to the Nc of whole plant. Hence the N status (content) is the main factor for the regulation of P_{sat} in both the individual leaves and the whole plant. However, since the coefficient of P_{sat}-Nc regression of individual leaves (Evans and Seemann 1989) or that of RGR-Nc regression of the whole plant may differ among species, the reason for the difference in regression coefficient should be determined.

P_{sat} is closely related to the photosynthate translocation from leaves (Hofstra and Nelson 1969, Stephenson *et al.* 1976) which indicates that the net carbon translocation rate (CFR) from leaves is one of the factors that regulate P_{sat}. When the photosynthate translocation is inhibited, photosynthates accumulate in leaves. This inhibits photosynthesis by a feedback system (*e.g.*, Krapp and Stitt 1995) that works as follows: (*1*) Starch granules are disrupted and starch concentration increases, which results in an increase in mesophyll CO_2 diffusion resistance (Nafzinger and Koller 1976, Cave *et al.* 1981, Grub and Mächler 1990). However, this assumption is unlikely, because Huber and Hanson (1992) reported that photosynthesis was inhibited in a starch-less mutant. (*2*) The synthesis of sucrose and/or re-circulation of hexose results in a large increase of phosphate intermediates, which decreases the level of inorganic phosphates. This implies that the low concentration of inorganic phosphates in the chloroplast inactivates RuBPCO (Heldt *et al.* 1978) and decreases the ATP/ADP ratio, which leads to the inactivation of RuBPCO (Sharkey 1990). (*3*) The concentration of saccharides regulates the photosynthetic rate through the expression of genes (Sheen 1989, Schäfer *et al.* 1992, Krapp *et al.* 1993). Hence, emphasis should be placed on the relationship between P_{sat} and the photosynthesised ^{14}C-translocation rate.

Thus, P_{sat} has a significant linear relationship with Nc, however, P_{sat}-Nc regression coefficient is different among crops, which is not explained appropriately by now. Carbon translocation from leaves is another possible factor of P_{sat}. Therefore, we hypothesise that P_{sat} is regulated by two factors, Nc (component factor) and translocation of N or C compounds (translocation factor). To elucidate this hypothesis, we examined the interrelationship between P_{sat} and translocation of ^{14}C- or ^{35}S-compounds.

Materials and methods

Plants: Rice (*Oryza sativa* L.), winter wheat (*Triticum aestivum* L.), spring wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], adzuki bean (*Phaseolus angularis* L.), potato (*Solanum tuberosum* L., a cross of *Solanum tuberosum* L., and *Solanum andigenum* L.), sugar beet (*Beta vulgaris* L.), sunflower (*Helianthus annuus* L.), *Maackia amurensis* var. *bergeri* C.K. Schn., *Prunus sargentii* Rehd., and *Populus maximowiczii* Henry were grown in the field of the Faculty of Agriculture, Hokkaido University, Sapporo, Japan (43°03′N, 141°20′E).

$^{14}CO_2$ and ^{35}S-methionine translocation in individual leaf: In 1996, wheat, maize, soybean, *M. amurensis* var. *bergeri*, *P. sargentii*, and *P. maximowiczii* were planted in 4 000 cm^3 pots filled with alluvial soil in a greenhouse (natural irradiation and uncontrolled temperature) of Hokkaido University. As fertilisers, 1 g N (ammonium sulfate), 1 g P_2O_5 (superphosphate), and 1 g K_2O (potassium sulfate) per pot were applied.

A fully expanded leaf of each plant was covered with a clear polyethylene bag. Then $^{14}CO_2$ was liberated for 10 min under natural irradiation by mixing 1 cm^3 of 0.18 mM $NaHCO_3$ with 3.7 MBq [2.2 GBq $mmol^{-1}$ ($NaH^{14}CO_3$ solution)] and 5 cm^3 of 0.3 kg m^{-3} $HClO_4$ in the bag. 2 h after $^{14}CO_2$ assimilation, the translocation of ^{14}C to petiole and stem (negligible in other organs) was estimated. ^{35}S-methionine [0.37MBq, 0.56 GBq $mmol^{-1}$ (^{35}S-methionine in phosphate buffer, pH 7.5)] was applied to leaf tip. The tip of fully expanded leaf of each plant was cut with a sharp razor in water. Then the leaf tip was immediately soaked in the ^{35}S-methionine in phosphate buffer (pH 7.5) for 1 h, and 2 h after ^{35}S introduction the leaf was sampled. The amounts of total ^{14}C and ^{35}S were determined by the method of Shinano *et al.* (1996). The translocation rate was determined by the change of radioactivity in the leaf.

At the same day, P_{sat} was measured in a fully expanded leaf using a portable infrared gas analyser (*LCA-3, The Analytical Development Co.*, England). P_{sat} was measured at 1 500 µmol m^{-2} s^{-1} produced by a halogen lamp (*KTS-100R, Kenko Co.*, Japan).

To estimate nitrogen content (Nc) changes of individual leaf by the Kjeldahl method, corresponding leaves were sampled at one week intervals from leafing to senescence. Nc after full expansion was expressed by a function of time as follows:

$$\mathrm{Nc} = \mathrm{Nc}_0 \exp(-\mathrm{Nf}\, t) \qquad (1a)$$

where Nf is a coefficient, t is the number of days after leafing, and Nc_0 is the initial value. As the Nc value converges finally with the Nc value of dead leaf (Ncd), the Eq. (1a) can be modified to

$$\mathrm{Nc} = (\mathrm{Nc}_0 - \mathrm{Ncd}) \exp(-\mathrm{Nf}\, t) + \mathrm{Ncd} \qquad (1b)$$

Based on the assumption that Nc is related to the net balance of N influx and translocation from individual leaves, the net N translocation rate (NFR) is calculated from Eq. (1b) as

$$\mathrm{NFR} = \Delta(\mathrm{Nc} - \mathrm{Ncd})/\Delta t = -\mathrm{Nf}\,(\mathrm{Nc} - \mathrm{Ncd}) \qquad (2)$$

Table 1. List of cultivars or lines and nitrogen application [g(N) m^{-2}] in various crops for estimating RGR. References: a – Morikawa (1990), b – Matsumoto (1992), c – Res. Rep. Central Agr. Exp. Stat. (Hokkaido Pref.) **1973**: 29-33, 1973, d – Res. Rep. Central Agr. Exp. Stat. (Hokkaido Pref.) **1976**: 29-41, 1976, e – Matsumoto (1994), f – Ohashi (1994), g – Res. Rep. Central Agr. Exp. Stat. (Hokkaido Pref.) **1980**: 43-47, 1973, h – Yoshimura (1988), i – Hirai (1957), Yamanouchi (1963), k – Kawamukai (1994). Authors not cited in References were graduate or undergraduate students in the Laboratory of Plant Nutrition, Faculty of Agriculture, Hokkaido University.

	Cultivars or lines	New or old	N application	Density [cm×cm] or spacing [grain m^{-2}]	Reference	Symbols in Figs. 2 & 3
Rice	Jyoiku	New	20	30×15	a	●
			10	30×15	b	▶
	Michikogane	New	10	30×15	a	◆
	Yunami	Old	10		c	○
	Eikou	Old	10		c	◇
Winter wheat	Tsukisamu	New	19	250	a	●
			20	250	b	▶
	Horoshiri	New	20	250	b	▲
	Mukakomugi	Old	8		d	Δ
Spring wheat	M27	New	20	200	e	●
			30	200	f	▲
	Haruhikari	Old	8		g	○
Maize	P3540	New	25	40×30	a	●
			20	40×30	b	▶
	P3732	New	20	40×30	b	▲
	Wisconsin No. 80	Old	10		h	○
Soybean	Kitamusume	New	20	50×20	a	●
	Tsurukogane	New	30	50×20	f	
			30	50×20	e	▲
			30	50×20	e	▼
	Oyathi No. 2	Old	8		i	○
	Tokachinagaha	Old	8		i	◇
Adzuki bean	Takarashouzu	Old	2.5		j	○
Potato	W80135-40	New	15	30×20	b	▲
			15	30×20	b	▼
	Dansyakuimo	Old	10		h	○
			30		h	◇
Sugar beet	Sugarman gold	New	30	30×25	b	▲
	Monohomare	New	30	30×25	b	●
Sunflower	Hokuren	New	20	40×30	b	●
			20	40×30	b	◆
	Russia	Old	20	40×30	b	○
			20	40×30	b	◇
Maackia amurensis			10	100×100	k	
Prunus sargentii			10	100×100	k	
Populus maximowiczii			10	100×100	k	

Changes of relative growth rate and N content in the canopy: At one-week intervals (5 stages or more, depending on plant species), 4 to 8 plants were collected, separated into leaves, stems, and harvesting organs, and dried for 48 h at 80 °C in an air-forced oven. Their mass was then determined and they were ground. The list of crops, cultivars, or lines, as well as the N application rate, is in Table 1. The experimental design was a randomised complete block with two replications. Each plot consisted of a 5×20 m area.

RGR of the canopy leaves was calculated by the following equation:

$$\mathrm{RGR} = (1/M)\,(dM/dt)$$

where M is plant dry mass [g m^{-2}], and t is diurnal time.

Results

Translocation of ^{35}S and ^{14}C: The translocation rate of ^{35}S-methionine, which is used as a representative compound for the translocation of N compounds, was positively correlated with the translocation rate of $^{14}CO_2$-assimilates (Fig. 1), indicating that the translocation of C and N compounds from leaves is interrelated. Since P_{sat} was related significantly with ^{14}C-translocation rate (Fig. 1), high P_{sat} was supported by high ^{14}C-translocation rate. Hence the high P_{sat} of maize was supported by the high translocation rate of C compounds from the leaves. Even when the values on maize were omitted from Fig. 1, P_{sat} showed a positive significant relationship with the ^{14}C-translocation rate.

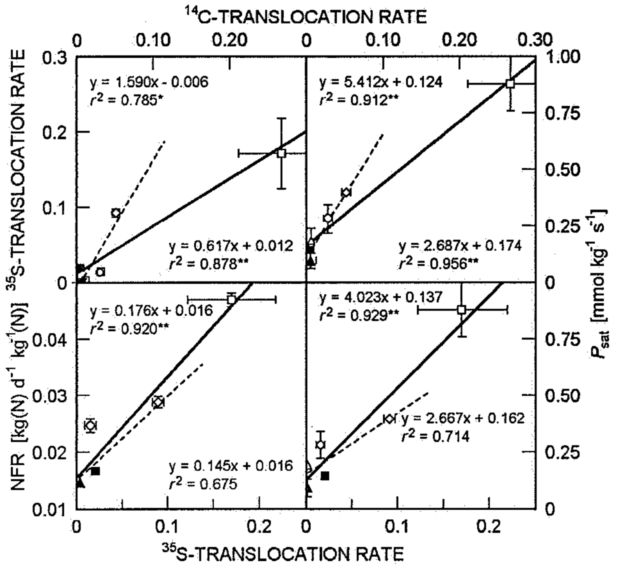

Fig. 1. Relationship between ^{14}C translocation rate and photosynthetic rate, ^{35}S translocation rate and NFR, and ^{14}C and ^{35}S translocation rate in: ◊ winter wheat, □ maize, ○ soybean, ▼ *Maackia amurensis*, ■ *Populus maximowiczii*, ▲ *Prunus nipponica*. Bars in the figure indicate SE value (when SE value was less than 0.05, bars were not used). **significant at 1 % level, *significant at 5 % level. ——— regression including all the species, – – – regression except for maize.

NFR had a significant relationship with ^{35}S-translocation rate (Fig. 1), indicating that NFR is one indicator for re-translocation of nitrogen compounds from leaves. ^{35}S-translocation rate was also significantly related with P_{sat} (Fig. 1).

Relationship between RGR and N content in leaf canopy: Nc in leaf canopy decreased exponentially with the progress of growth (Fig. 2), of which pattern was similar to that of single leaf (Osaki *et al.* 2001). Therefore, Nc was expressed by Eq. (1a) at 1 % significance level.

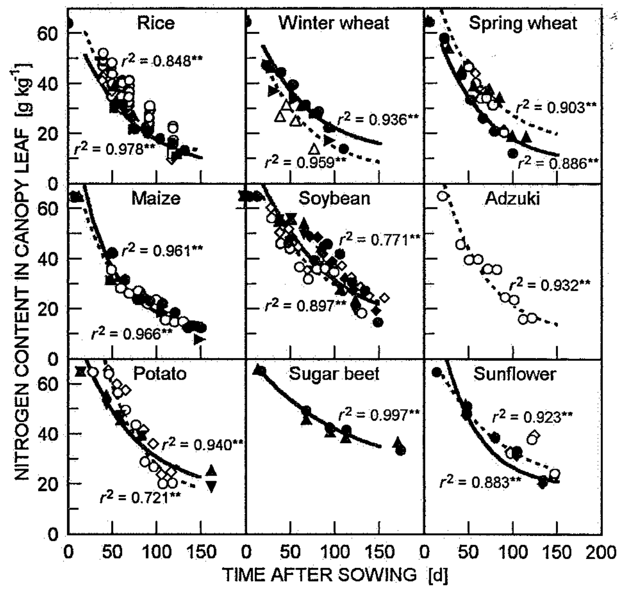

Fig. 2. Changes in nitrogen content of leaf canopy at successive growth stages. Symbols are indicated in Table 1. Regressions are estimated from Eq. (1b) within old (– – –) and new (———) cultivars due to the small variation within old or new cultivars. **significant at 1 % level.

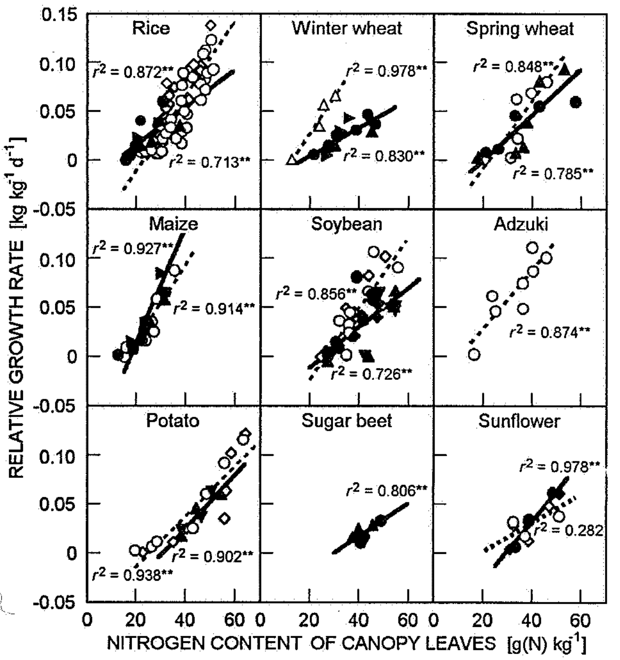

Fig. 3. Relationship between relative growth rate (RGR) and nitrogen content in leaf canopy. Symbols are indicated in Table 1. Regressions are estimated from Eq. (4) within old (– – –) and new (———) cultivars due to the small variation within old or new cultivars. **significant at 1 % level.

The Nc of leaf canopy including dead leaves was linearly related with RGR (Fig. 3). RGR was expressed as

$$\mathrm{RGR} = \mathrm{DMf\,Nc} + \mathrm{RGR}_0 \qquad (3)$$

where Nc is the nitrogen content in leaf canopy including dead leaves, and DMf and RGR_0 are coefficients.

Discussion

Net C and N translocation from individual leaf: Since NFR is related to the ^{35}S-translocation rate (except in soybean, Fig. 1), NFR may be a useful indicator of the translocation rate of N compounds. Thus, NFR is regulated also by Nc and Nf, indicating that if Nf is high or low, the net N translocation rate per unit Nc is high or low, respectively. The translocation rate of ^{35}S-methionine, which is used as a representative compound for the translocation of N compounds, was also positively correlated with the translocation rate of $^{14}CO_2$-assimilates (Fig. 1), indicating that the translocation of C and N compounds from leaves is interrelated.

P_{sat} after full expansion is closely related to the net translocation rate of carbon compounds from individual leaves (CFR) for the following reasons: (*1*) If P_{sat} exceeds CFR, the leaf dry mass should increase with the progress of growth, nevertheless, LMA remained constant during growth or decreased (Osaki *et al.* 2001). (*2*) Hofstra and Nelson (1969) and Stephenson *et al.* (1976) reported that P_{sat} is closely related to the rate of photosynthate translocation. We also found that P_{sat} was closely related to the ^{14}C-translocation rate from individual leaf (Fig. 1), indicating that CFR could be estimated from P_{sat}.

In our previous observations, the P_{sat} of crops decreased linearly with the decrease of Nc except in the early leafing stage (Osaki *et al.* 2001), and the P_{sat} (or CFR)-Nc relationship was as follows:

$$P_{sat}\ (\text{or CFR}) = \mathrm{Cf\,Nc} + P_{sat0}\ (\text{or } \mathrm{CFR}_0) \qquad (4)$$

where Cf, P_{sat0}, and CFR_0 are constants. Thus P_{sat} (or CFR) is regulated by both Nc and Cf. The variation in Cf depending on the leaf position was small (Osaki *et al.* 2001).

Relationship between RGR and Nc in leaf canopy: According to Ingestad (1977, 1979), RGR was in a linear relation with the Nc of the whole tree. This was not confirmed by Greenwood *et al.* (1991) for whole plant in field crops, and in our results except for rice, RGR reached a hyperbolic ceiling when the Nc of whole plants at all ages increased (values not shown). In contrast to the Nc of whole plants, the Nc of the leaf canopy including dead leaves displayed a significant linear relationship with RGR (Fig. 3). Thus the RGR-Nc regression of the whole plant (Eq. 3) was expressed in a pattern similar to that of the CFR-Nc regression of individual leaves (Eq. 4). In addition, when the net assimilation rate and Nc were expressed on a leaf area basis, the CFR-Nc relationship throughout the growth stages became ambiguous (values not shown) because the leaf mass per area (LMA) changed over the course of growth. Therefore, in the current report, RGR was used rather than NAR as a parameter of the photosynthetic rate of whole plant.

Since Nc of the leaf canopy decreased exponentially with growth, it was expressed by a function of time (diurnal) as indicated in Eq. 1 (Fig. 2). NFR of the leaf canopy was also estimated by using Eq. 2, indicating that the NFR of the leaf canopy is a function of the Nc of the leaf canopy.

DMf in all examined crops showed a clear relationship with Nf of leaf canopy (Fig. 4). Thus the net C translocation from leaf canopy per unit of Nc was closely related to the net N translocation from leaf canopy per unit of Nc. We also estimated Cf and Nf of individual leaves using values reported in Osaki *et al.* (2001). It was confirmed that Cf-Nf of individual leaves had also significant relationship similar to that of DMf-Nf of canopy.

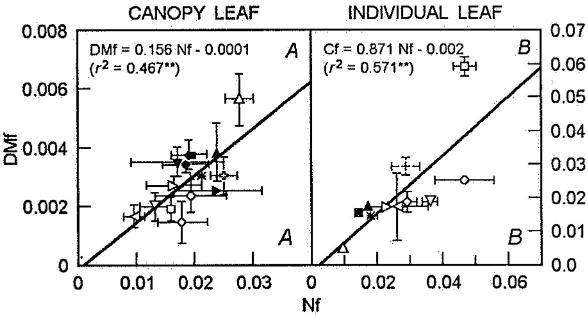

Fig. 4. Relationship between Nf and DMf of canopy (*A*) or between Nf and Cf of individual leaf (*B*). Bars in the figure indicate SE value. Nf and Cf of individual leaves were calculated from values reported in Osaki *et al.* (2001). Symbols in *A* are (*open symbols*: new cultivars, *closed symbols*: old cultivars): □ rice, ◊ winter wheat, ○ spring wheat, Δ maize, ∇ soybean, ▷ potato, ◁ sugar beet, ✤ sunflower. Symbols in *B*: + rice, ◊ winter wheat, □ maize, ○ soybean, ∇ field bean, ◁ tomato, ▷ potato, * sugar beet, Δ *Maackia amurensis*, ■ *Populus maximowiczii*, ▲ *Prunus nipponica*. **significant at 1 % level.

Thus, ^{14}C and ^{35}S translocation, DMf-Nf relationship, and Cf-Nf relationship indicate that P_{sat} (or CFR) may be explained by Nc and net N translocation from leaves. A relatively higher P_{sat} can be accompanied by a relatively higher rate of net N decrease in individual leaves or whole canopy leaves. If the N decrease of leaves is high, leaf senescence is accelerated; hence the difficulty of maintaining a relatively high RGR.

The relationship between leaf longevity and P_{sat} was confirmed by Bazzaz and Pickett (1980), Chabot and Hicks (1982), Coley *et al.* (1985), Koike (1988), Field and Mooney (1986), and Reich *et al.* (1992, 1995). In accordance with these studies, we found also a negative correlation of leaf longevity with P_{sat} (Fig. 5). Since the net C translocation rate (or photosynthetic rate) is closely related to the net translocation rate of N compounds, it is assumed that leaf longevity decreases or increases when P_{sat} is high or low, respectively, because N is actively or slowly translocated from leaves in correspondence to a high or low P_{sat}.

Cf and Nf showed a negative relationship with leaf longevity (Fig. 5). Thus, a high photosynthetic rate is supported by a high translocation rate of C and N compounds from leaves. Since a high Nf reflects a high net N re-translocation rate from leaves, leaf senescence is accelerated, because the senescence of a leaf is usually accompanied by a decrease of Nc in a leaf (Mooney *et al.* 1981, Field 1983). Based on the above results, we assume that a high P_{sat} is a cause of shortened leaf longevity, because a high P_{sat} followed a high Nc decreasing rate and *vice versa*. Thus we suggest that P_{sat} is closely related to leaf longevity. In a canopy, new (high-yielding) cultivars were improved toward increased leaf longevity, and NAR remained relatively low. In fact, high yield was attained due to the high leaf area duration (LAD) and not to a high NAR (Osaki *et al.* 1991, 1993). NAR was negatively correlated with LAD (Osaki *et al.* 1993, except for soybean), which was attributed to the fact that a high NFR resulted in a relatively high P_{sat} (high NAR), while high NFR was ascribed to rapid leaf senescence (low LAD).

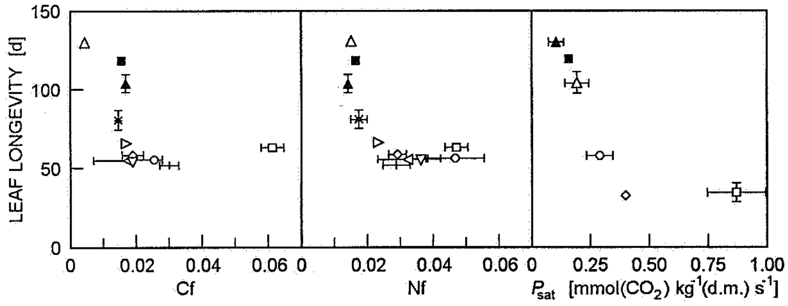

Fig. 5. Relationship between leaf longevity and Cf, Nf, and maximum P_{sat} in individual leaves. Bars in the figure indicate SE value. Cf and Nf were cited from Fig. 4, and maximum P_{sat} was estimated from average value of maximum P_{sat} in individual leaves reported in Osaki *et al.* (2001). Leaf longevity of individual leaves is the estimated date from leafing to senescence, then average value of leaf longevity was calculated. Symbols in the figure are the same as in Fig. 4*B*.

Conclusion: We demonstrated that P_{sat} or RGR in all the examined crops was regulated primarily by two factors: (*1*) by Nc in leaves, which is related to the RuBPCO and chlorophyll contents; and (*2*) by net N translocation from leaf per unit of Nc (Nf). As a result, the net N translocation rate from leaves (NFR) is related to leaf senescence, which depends on the N status in the leaves. Thus, P_{sat}, NFR, and leaf senescence are interrelated. Since fast-growing plants develop systems in which the leaf N is actively re-translocated from lower to upper leaves or apical organs, the leaves on top of the canopy develop most easily (Hirose *et al.* 1989). This ecological strategy of fast-growing plants can be explained using our model. Further, this sequential N re-translocation from lower to upper rice leaves is strongly regulated by an inherent mechanism (Tanaka 1961). As a result, leaves with the highest activity are being continuously constructed at the canopy top, which phenomenon is called the "active centre leaf theory" in rice plant (Tanaka 1961). In other words, fast-growing plants have to construct a continuously active centre at the top of the canopy to compete with other plant species; thus N was re-translocated actively from lower to upper leaves. It is, therefore, concluded that the relationship of P_{sat} (or RGR)-NFR-leaf senescence reflects the different ecological strategies of fast-growing and slow-growing plants. Consequently, we propose a new model for plant growth (P_{sat} and RGR), regulated by cumulative N status (content) in the leaves and by N dynamics (translocation) in individual leaves (canopy leaves). Previously, it was difficult to explain RGR of the canopy by the P_{sat} of single leaf. Our model, however, elucidates that RGR of the canopy is explained by the P_{sat} of single leaf if, for that leaf, N status (concentration in the leaf) and nitrogen dynamics (N translocation from the leaf) are both estimated.

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