

## Slow Leaf Development of Evergreen Broad-leaved Tree Species in Japanese Warm Temperate Forests

SHIN-ICHI MIYAZAWA\*†, SHIGENARI SATOMI‡ and ICHIRO TERASHIMA§||

\* Department of Biology, Faculty of Science, Chiba University, 1-33 Yayoi-Cho, Inage-Ku, Chiba, 263-0022 Japan,

† University Forest in Chiba, Faculty of Agriculture, University of Tokyo, Amatsu, Amatsukominato-Machi, Awa-Gun, Chiba, 299-5503 Japan and § Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki, 305-0006 Japan

Received: 6 May 1998 Returned for revision: 6 July 1998 Accepted: 24 August 1998

Rates of light-saturated net photosynthesis ( $P_N$  max) and dark respiration (Rd) on a leaf area basis, leaf dry mass per area (LMA), leaf nitrogen content on a leaf area basis (LNa) and instantaneous nitrogen use efficiency ( $NUE = P_N \text{ max}/LNa$ ) were followed during leaf development in six evergreen broad-leaved tree species typical of warm-temperate forests in Japan. These species were *Castanopsis sieboldii*, *Quercus myrsinaefolia*, *Quercus glauca*, *Machilus thunbergii*, *Cinnamomum japonicum* and *Neolitsea sericea*. When expansion of leaf area was complete,  $P_N$  max was about one third of its peak value and increased for another 15 to 44 d. Rd at full leaf expansion was about 1.5 to 3.5-times greater than steady-state rates. These facts suggest that leaf development was still underway at the time of full leaf area expansion. Low  $P_N$  max at full leaf expansion was caused both by low leaf nitrogen content and low NUE.  $P_N$  max increased with the increase in LMA during leaf development in all six species; data from the literature for other species with different life forms also indicated a similar tendency. The steady-state LMA varied markedly among species. Because leaves with larger steady-state LMAs need more resources for their construction, they will also need longer periods for maturation. We hypothesized that the period required for the attainment of peak  $P_N$  max, the 'leaf maturation period', depends on the steady-state LMA. Plotting data from the present study together with those from literature for other plants across several life forms showed a strong positive relationship between leaf maturation period and steady-state LMA, supporting the hypothesis.

© 1998 Annals of Botany Company

**Key words:** *Castanopsis sieboldii*, *Cinnamomum japonicum*, delayed period, expansion period, full leaf expansion, *Machilus thunbergii*, maturation period, *Neolitsea sericea*, *Quercus glauca*, *Quercus myrsinaefolia*, steady-state LMA.

### INTRODUCTION

It has been widely recognized that net photosynthesis at light saturation expressed on a leaf area basis ( $P_N$  max) peaks at or before the completion of leaf area expansion (Šesták, 1985). This phenomenon has been reported in cucumber (*Cucumis sativus* L.; Ho *et al.*, 1984), bean (*Phaseolus vulgaris* L.; Čatský, Tichá and Solárová, 1976) and some deciduous broad-leaved trees from Japanese cool-temperate forests (Koike, 1990). However,  $P_N$  max peaks well after the completion of leaf expansion in some other species, including cocoa (*Theobroma cacao* L.; Baker and Hardwick, 1973), coffee (*Coffea arabica* L.; Yamaguchi and Friend, 1979), mango (*Mangifera indica* L.; Lee, Brammeier and Smith, 1987), kiwifruit (*Actinidia deliciosa* var. *deliciosa* L.; Buwalda, Meekings and Smith, 1991), and shade tolerant, 'delayed greening' species in tropical rainforests (Kursar and Coley, 1991, 1992*a, b*).

Kursar and Coley (1992*b, c*) studied leaf developmental

patterns in several species from a tropical rain forest and distinguished 'delayed' greening species from 'normal' greening species. Normal greening species, which showed maximum rates of leaf photosynthesis at or near full leaf expansion, were found only in sunny habitats while delayed greening species were found in shaded understorey where the cost for forfeited photosynthesis (low chlorophyll and Rubisco content of expanding leaves) would be low. Delayed greening is suggested to be an effective strategy against herbivory: by delaying the transport of valuable resources such as nitrogen into the lamina until a leaf is fully expanded and leaf structure becomes tough, plants may minimize the loss of resources caused by herbivory. Since the damage to young leaves is higher in rainforests than in any other forest type (Coley and Aide, 1991), Coley and Kursar (1997) suggested that species with delayed greening had been selected under conditions of low PPFD (less than 1% of full sunlight) and high herbivory typical of the understorey of tropical lowland rainforests. They speculated that such species might be rare under higher PPFD conditions for the above reason (Coley and Kursar, 1997).

Young leaves of delayed greening species are red, brown or white and these species show periodic shoot growth (Kursar and Coley, 1992*b*). These characteristics are also recognized in many evergreen broad-leaved trees of warm-temperate

† For correspondence at: Department of Biology, Graduate School of Science, Osaka University, 1-16 Machikaneyama-Cho, Toyonaka, Osaka, 560-0043 Japan. Fax +81-6-850-5808, e-mail miyazaw8@chaos.bio.sci.osaka-u.ac.jp

|| Present address: Department of Biology, Graduate School of Science, Osaka University, 1-16 Machikaneyama-Cho, Toyonaka, Osaka, 560-0043 Japan.

forests in Japan. Many of these species, however, grow on sunny sites. In the present study, we examined leaf developmental patterns of some evergreen broad-leaved species in Japanese warm-temperate forests, and compared the patterns with those of tropical species with delayed greening. We followed changes in leaf area, rate of net photosynthesis at light saturation ( $P_N$  max) and dark respiration (Rd), both on a leaf area basis, leaf dry mass per area (LMA), leaf nitrogen content both on a dry mass basis (LN<sub>m</sub>) and on an area basis (LN<sub>a</sub>), and instantaneous nitrogen use efficiency ( $NUE = P_N \text{ max}/LN_a$ ) during leaf development in *Castanopsis sieboldii*, *Quercus myrsinaefolia*, *Quercus glauca*, *Machilus thunbergii*, *Cinnamomum japonicum* and *Neolitsea sericea*.

## MATERIALS AND METHODS

### Study sites and species

The study was carried out from September 1995 to September 1996 with six evergreen species on the Chiba University campus (35°36' N, 140°07' E, 20 m altitude) and the forest of the University of Tokyo on Mt. Kiyosumi (25°12' N, 140°09' E, 250 m altitude). Six evergreen species were studied: *Castanopsis sieboldii* (Makino) Hatusima ex Yamazaki et Mashiba (Fagaceae), *Quercus myrsinaefolia* Blume (Fagaceae), *Machilus thunbergii* Sieb. et Zucc. (Lauraceae) and *Neolitsea sericea* (Bl.) Koidz. (Lauraceae) on the Chiba University campus, and *Quercus glauca* Thunb. ex Murray (Fagaceae) and *Cinnamomum japonicum* Sieb. ex Nakai (Lauraceae) in the Mt. Kiyosumi forest. These species are common in warm-temperate evergreen (laurel-leaved) forests in Japan, where they usually occupy canopy or subcanopy layers. A mature tree was selected for each species. All the trees except *N. sericea* were growing on open sites.

### Leaf expansion

Since leaf phenology differs within a single tree depending on its position, we selected two nearby branches in the sunniest parts of each tree crown in September 1995 (see Table 1 for light environment of the sample branches). In

TABLE 1. Relative photosynthetic photon flux density (RPPFD) immediately above the apical buds of the branches used for the continuous size measurement

	RPPFD (%)
<i>Castanopsis sieboldii</i>	40.1 ± 19.9
<i>Quercus myrsinaefolia</i>	51.1 ± 17.6
<i>Quercus glauca</i>	41.5 ± 8.5
<i>Machilus thunbergii</i>	65.1 ± 32.9
<i>Cinnamomum japonicum</i>	36.0 ± 11.7
<i>Neolitsea sericea</i>	4.9 ± 1.9

Each value indicates the mean ± s.d. for 14 to 27 apices. Photosynthetic photon flux density (PPFD) was measured at least twice for each apex before bud break in April 1996. The measurement was carried out at 1200 h on a cloudy day.

the *Castanopsis sieboldii* tree, we also selected two shaded branches. These sets of two branches had between 14 and 27 current-year shoots. We tagged every node bearing current-year leaves, and measured the length of all winter buds on current-year nodes once or twice a week. In April 1996, before bud break, we measured relative photon flux density (RPPFD) immediately above the top of the apical buds of the sample branches (Table 1). After bud break in 1996, we measured the length of new stems and leaf blades continuously.

Leaf area ( $A$ ) was calculated from the lamina length ( $L$ ) as:

$$A = aL + bL^2 \quad (1)$$

where  $a$  and  $b$  are constants for the respective species. The regression curve for each of the species was obtained based on  $L$  from 36 to 89 leaves sampled at various developmental stages. The coefficients of determination ( $R^2$ ) ranged from 0.88 to 0.99, and were all significant ( $P < 0.01$ ).

### Measurement of photosynthesis, leaf dry mass per area and leaf nitrogen

We measured the photosynthetic rate of leaves as described by Koike (1986). We selected two branches near the branches used for the continuous size measurement, and cut them under water. The branches were then taken to the laboratory. The leaf was cut under water at the base of the petiole, and the petiole inserted into a small cuvette filled with water. The leaf was irradiated with 'white light' of 700  $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  for about 30 min in air before the measurement. The rate of photosynthesis was measured with a portable gas-exchange system (SPBH3, Shimadzu, Kyoto, Japan, under the license of Analytical Development Co., Hoddesdon, UK) at an irradiance of 1200  $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  and a leaf temperature of  $27 \pm 1$  °C. Light was provided by a halogen lamp. The concentration of  $\text{CO}_2$  entering the chamber was kept at about 35 Pa. The rate of light saturated net photosynthesis ( $P_N$  max) was measured, as was the rate of dark respiration (Rd). At least two leaves were measured for each species at each sampling time. After the measurements, the area of the leaf blade was determined with an area meter (LI-3000A, Li-Cor, Lincoln, Nebraska, USA). Leaves were dried at 80 °C for about 48 h and weighed to determine leaf dry mass per area (LMA). Dried leaves were ground with a blender, and leaf nitrogen concentration was measured with a NC analyzer (NC-900, Shimadzu, Kyoto, Japan).

### Curve fitting

The changes in leaf area,  $P_N$  max, LMA, nitrogen content per leaf (NC per leaf) and NUE were fitted by logistic equations with the least squares method. The cessation date of leaf area expansion was defined as the date when more than 99% of the maximum leaf area was reached on the logistic equation, whereas the cessation dates of  $P_N$  max, LMA, NC per leaf and NUE were defined as the dates when more than 95% of the estimated maximum values were reached.

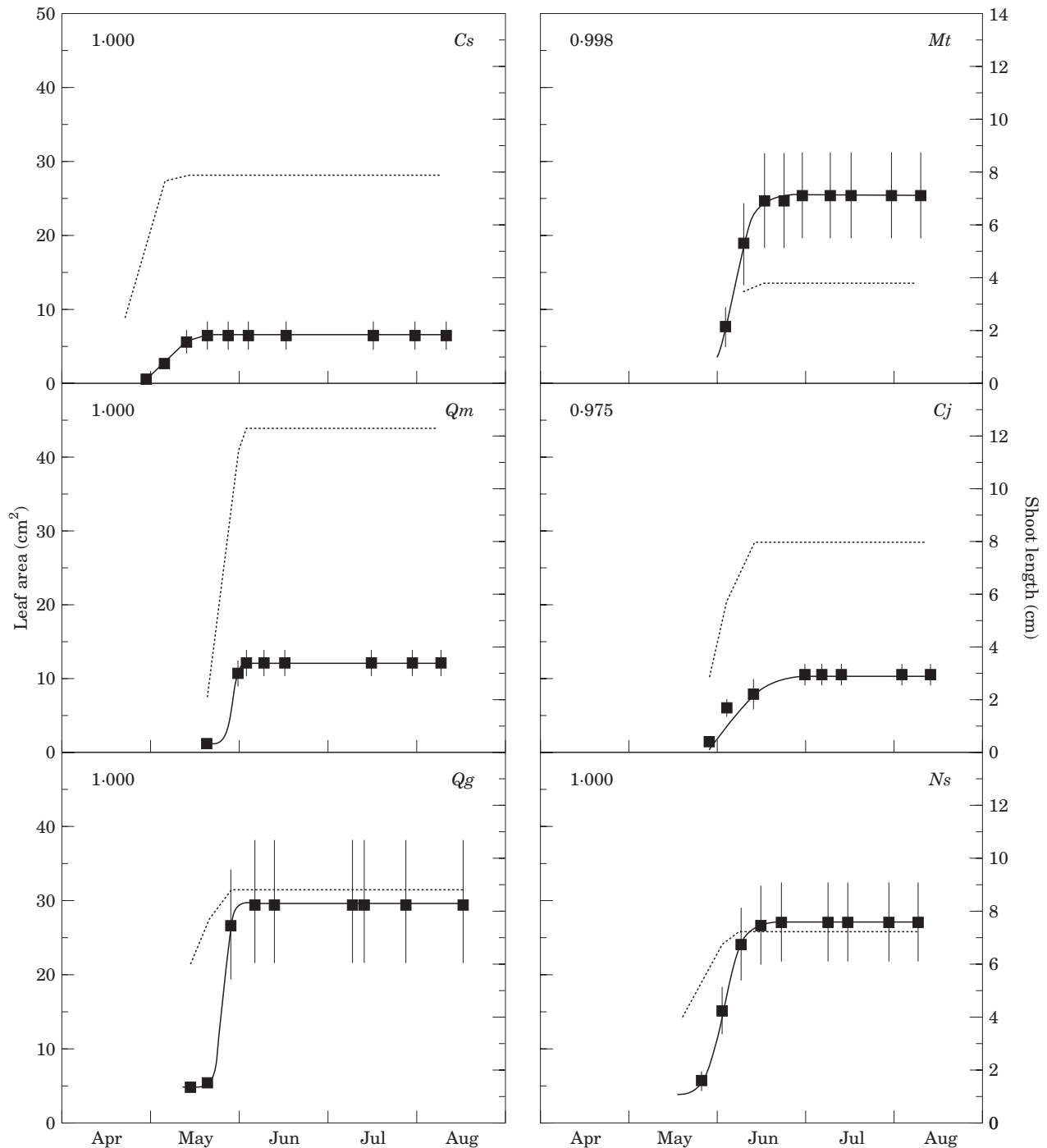


FIG. 1. Changes in leaf area (—) and shoot length (---) with time. Bars = s.d. Coefficient of determination ( $R^2$ ) for a logistic equation fitted to leaf area is given in the upper left of each panel.  $R^2$  is significant at  $P < 0.01$ . *Cs*, *Castanopsis sieboldii*; *Qm*, *Quercus myrsinaefolia*; *Qg*, *Quercus glauca*; *Mt*, *Machilus thunbergii*; *Cj*, *Cinnamomum japonicum*; *Ns*, *Neolitsea sericea*.

Rd and LN<sub>m</sub> decreased with time so we applied the equation as follows:

$$Y = c \exp(-dT) + e \quad (2)$$

where,  $Y$  is Rd or LN<sub>m</sub>,  $T$  is time after bud break, and  $c$ ,  $d$  and  $e$  are constants for each species.

The logistic equation and eqn (2) were also used to determine these values at full leaf expansion because they

fitted data very well (see determination coefficients given Figs 1, 2 and 3).

## RESULTS

### Changes in leaf area, $P_N$ max, Rd and LMA

In the six species studied, shedding of old leaves and flushing of new leaves occurred almost simultaneously. Leaf

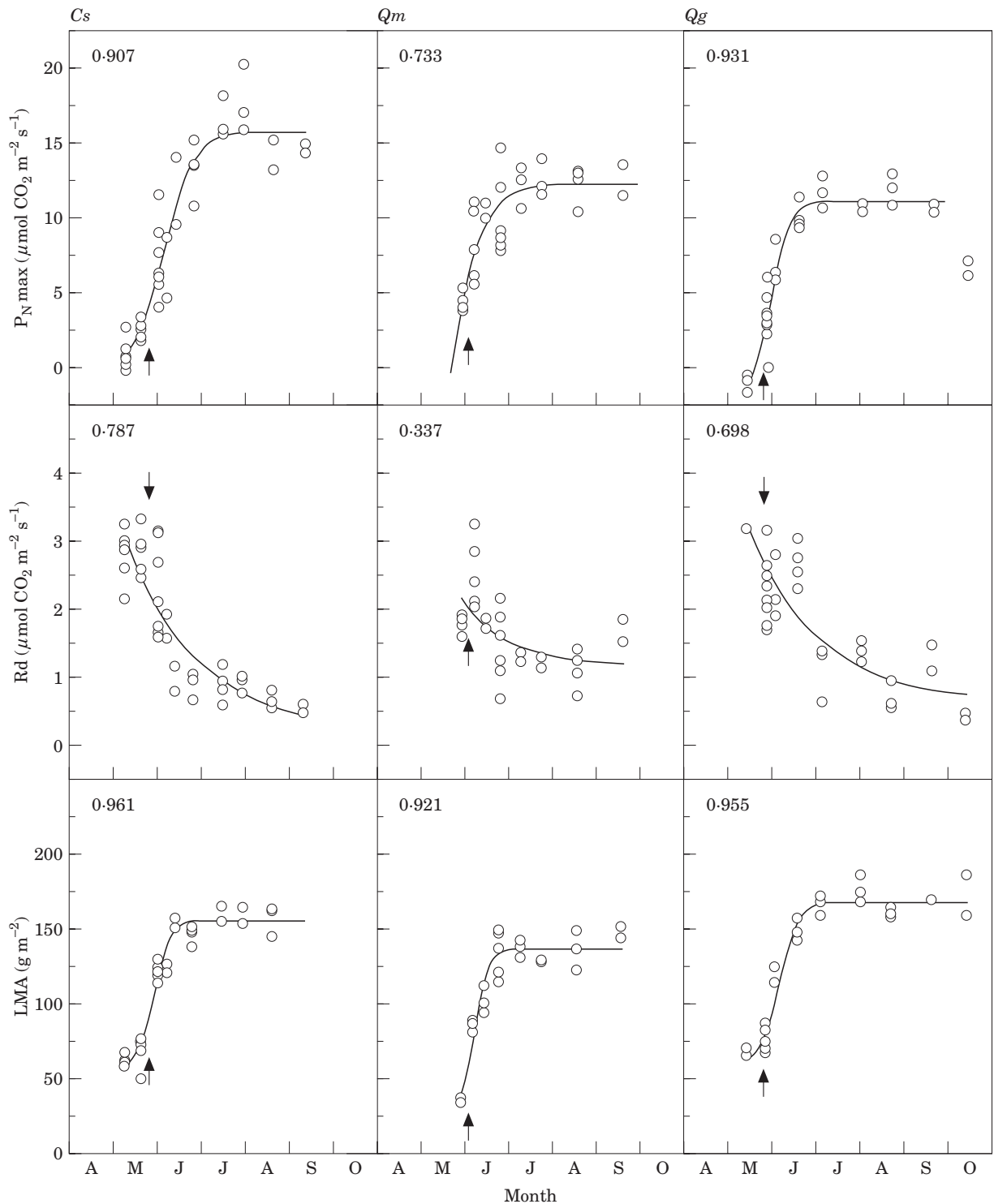


FIG. 2. For legend see facing page.

expansion ceased between late May and late June (Fig. 1). Changes in  $P_N$  max,  $R_d$  and LMA are shown in Fig. 2.  $P_N$  max increased with time and reached a plateau.  $P_N$  max did not reach its steady-state level at full leaf expansion in any of the species studied (indicated by the arrows). For

instance, in *C. sieboldii*,  $P_N$  max was  $3.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at full leaf expansion, while it was  $15.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the mature leaf. A period of approx. 43 d was required for *C. sieboldii* to 'mature' in terms of photosynthesis after full leaf expansion. For *Q. myrsinaefolia*, *Q. glauca*, *M.*

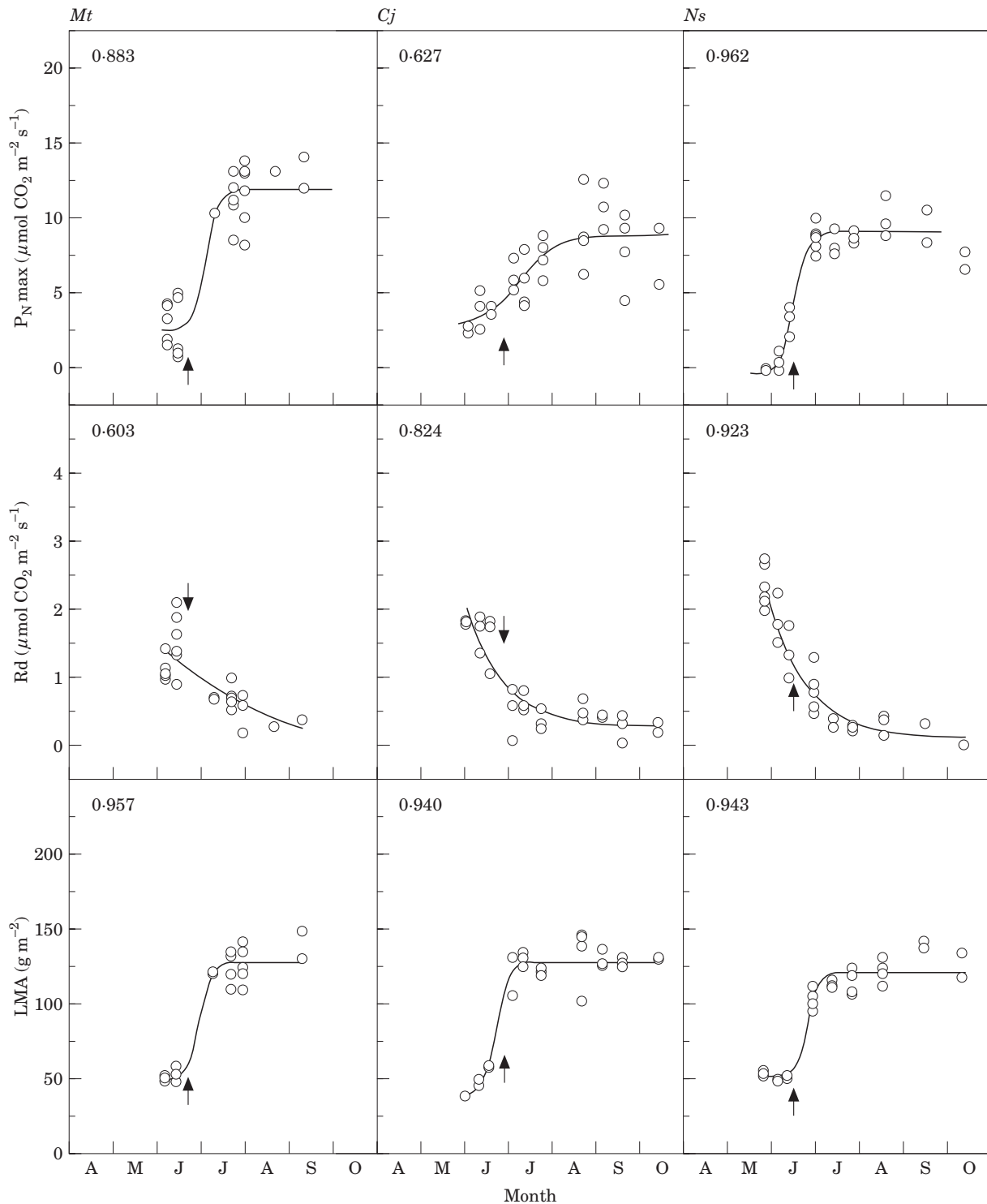


FIG. 2. Changes in the rate of net photosynthesis ( $P_N$  max) and dark respiration (Rd) both on a leaf area basis, and leaf dry mass per area (LMA) with time. Coefficient of determination ( $R^2$ ) for the logistic equation or eqn (2) is given in the upper left of each panel. Data collected in October were excluded for the curve fitting of the data of *Q. glauca* and *N. sericea*.  $R^2$  is significant at  $P < 0.01$ . Arrows indicate full leaf expansion. For abbreviations of species name see Fig. 1.

*thunbergii*, *C. japonicum* and *N. sericea*, approx. 32, 21, 24, 44 and 15 d, respectively, were required to reach photosynthetic maturity after full leaf expansion.

In all the species, Rd was highest at the beginning of leaf expansion and decreased gradually to a steady-state level. All six species still showed high Rd values at full leaf

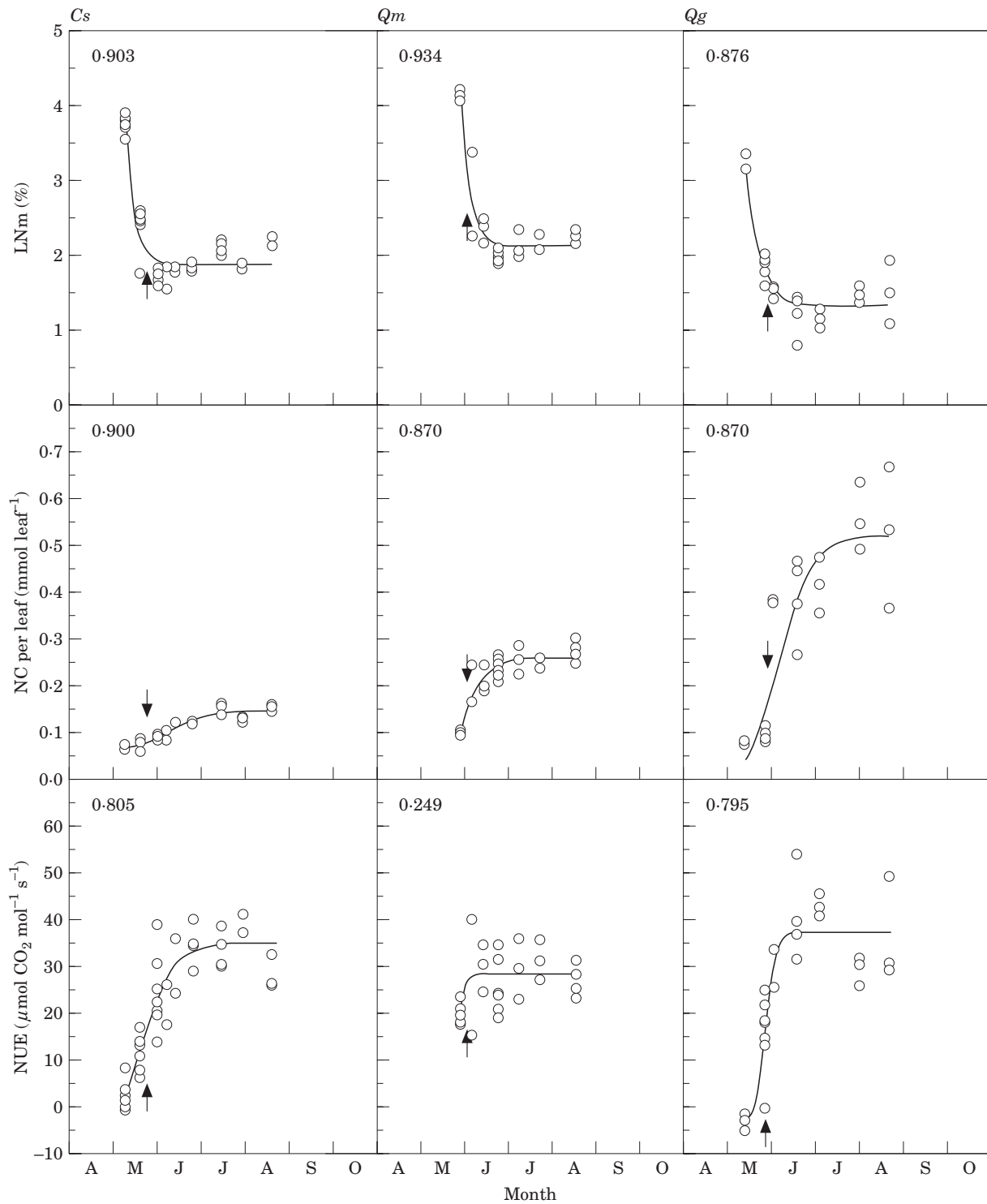


FIG. 3. For legend see facing page.

expansion (Fig. 2). These values were 1.5 to 3.5-times greater than the steady-state values in August. A long period was needed after full leaf expansion for the leaves to attain their steady-state  $R_d$  level.

Changes in LMA were similar to those in  $P_n$  max (Fig. 2). LMA increased rapidly after bud break, and reached a constant level from late June to early July. At full leaf expansion, LMA was far below the maximum.

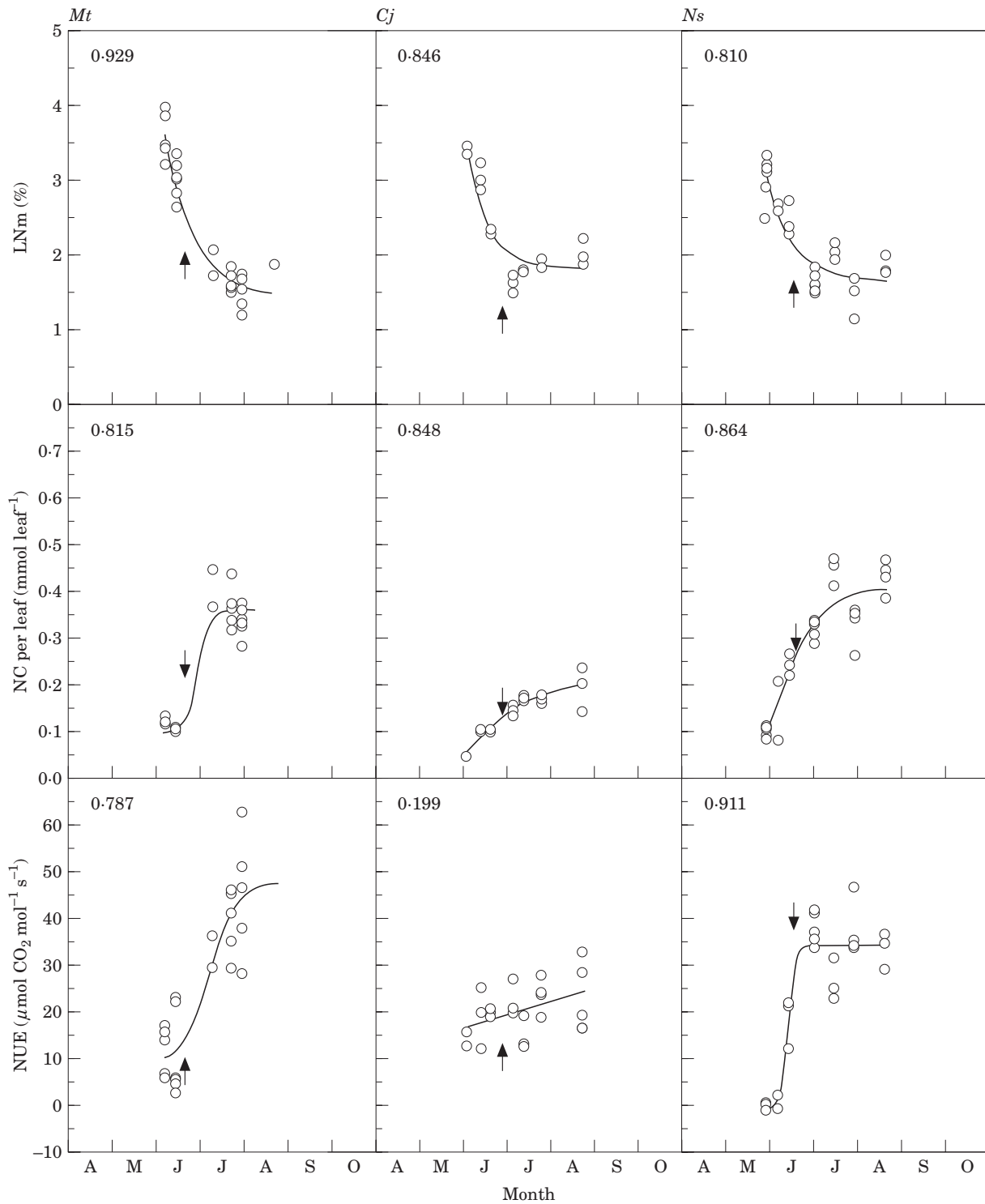


FIG. 3. Changes with time in leaf nitrogen concentration on a dry mass basis (LNm), nitrogen content per leaf (NC per leaf) and nitrogen use efficiency (NUE) during leaf development. The coefficient of determination ( $R^2$ ) is given in the upper left of each panel. All  $R^2$  values are significant at  $P < 0.01$  except LNm in *C. japonicum* ( $P < 0.05$ ). Arrows indicate full leaf expansion. For abbreviations of species names see Fig. 1.

#### Changes in LNm, NC per leaf and NUE

LNm (leaf nitrogen concentration on a dry mass basis) was highest at the early stage of leaf expansion. It then

decreased dramatically and almost reached the constant value soon after full leaf expansion (Fig. 3). The steady state value of LNm was  $1.69 \pm 0.31\%$  (mean  $\pm$  s.d. of all six species). In contrast, nitrogen content per leaf (NC per leaf)

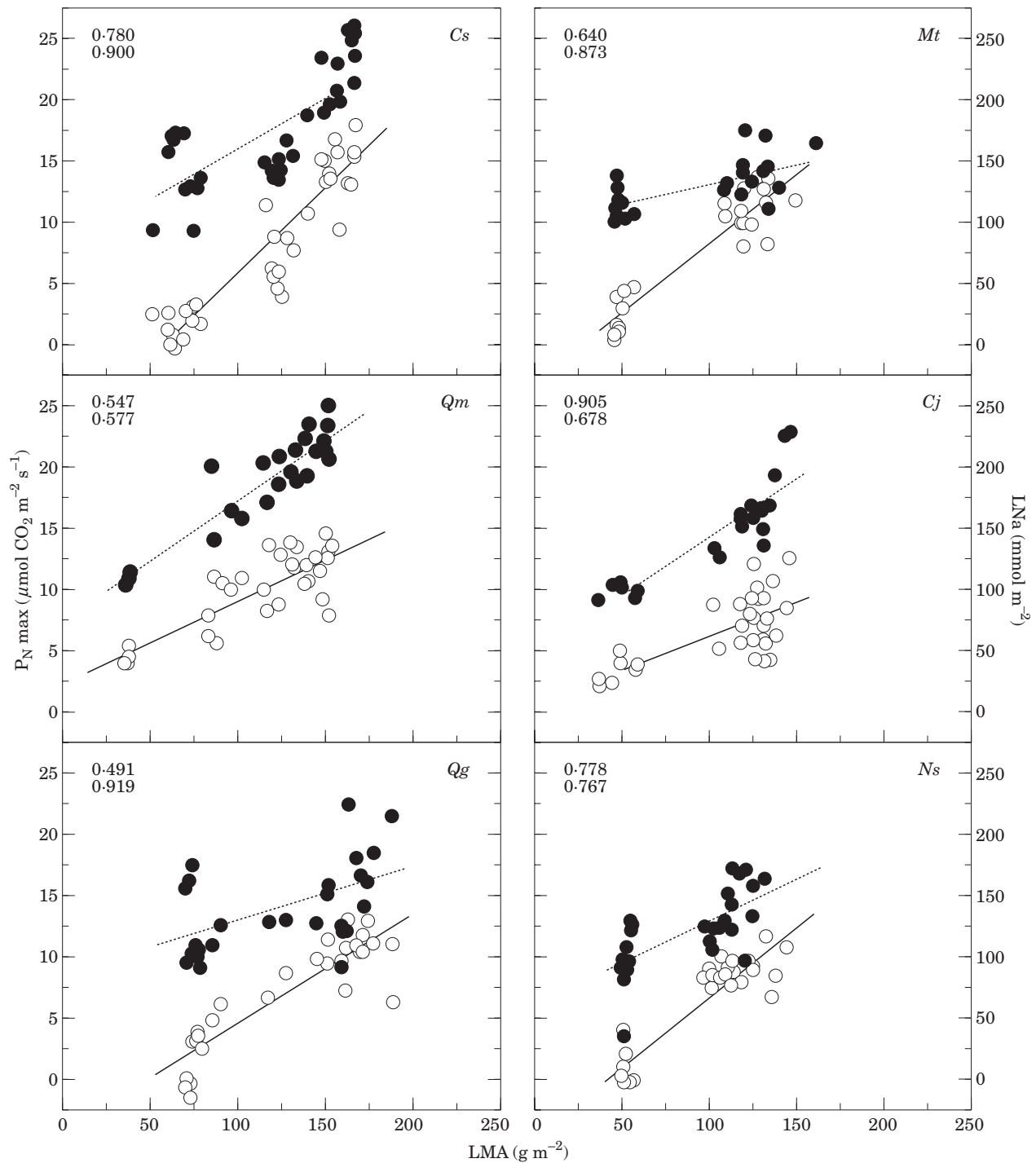


FIG. 4. The rate of net photosynthesis on an area basis ( $P_N \text{ max}$ ,  $\circ$ ) and nitrogen content on an area basis (LNa,  $\bullet$ ) as a function of leaf dry mass per area (LMA).  $P_N \text{ max}$  data for September and October were excluded. Upper and lower values in the top left of each panel are correlation coefficients between  $P_N \text{ max}$  and LMA, and LNa and LMA, respectively.  $r$  is significant at  $P < 0.01$ . For abbreviations of species names see Fig. 1.

showed a significant increase after full leaf expansion in all species.

NUE was low during leaf expansion and increased with time after full leaf expansion (Fig. 3). However, NUE did not change markedly during leaf development in *Q. myrsinaefolia* or *C. japonicum*.

#### Relationships between $P_N \text{ max}$ , LNa and LMA

In all species,  $P_N \text{ max}$ , LMA and NC per leaf increased well after full leaf expansion in a similar manner (Figs 2 and 3). There were significant positive correlations between  $P_N \text{ max}$ , LNa and LMA in all species (Fig. 4).



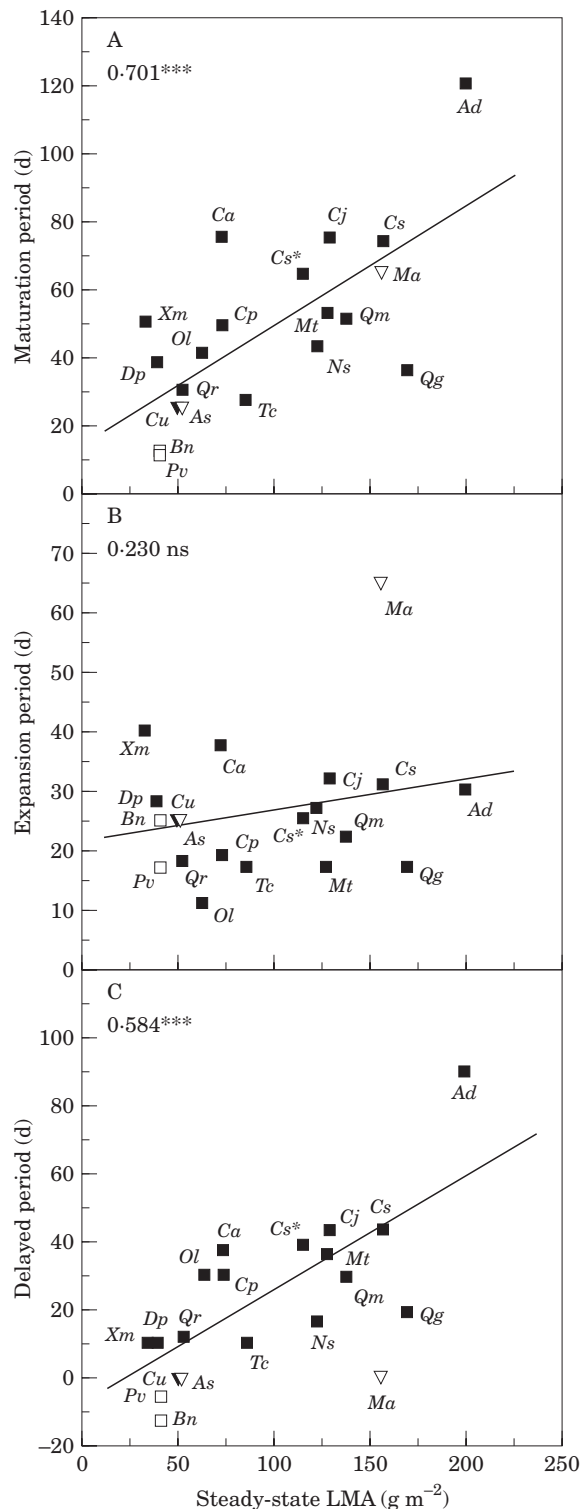


FIG. 5. Relationships between leaf maturation period (A), leaf expansion period (B), leaf delayed period (C) and steady-state leaf dry mass per area (steady-state LMA). Abbreviations for the six species studied are listed in Fig. 1. *Ad*, *Acitindia deliciosa* var. *deliciosa* L. (Buwalda *et al.*, 1991); *As*, *Annona spraguei* Saff. (Kursar and Coley, 1992b); *Bn*, *Brassica napus* L. (Jensen *et al.*, 1996); *Ca*, *Coffea arabica* L. (Yamaguchi and Friend, 1979); *Cp*, *Connarus panamensis* Griseb. (Kursar and Coley, 1992b); *Cs\**, *Castanopsis sieboldii* in the shade (in this study); *Cu*, *Cucumis sativus* L. (Ho *et al.*, 1984); *Dp*, *Desmopsis*

## DISCUSSION

### *Changes in photosynthetic characteristics and nitrogen content during leaf development*

For all species,  $P_N$  max and LMA increased with time and reached steady-state levels (Figs 2 and 3). The marked changes in these variables after full leaf area expansion are noteworthy because these trends contrast with the widely-held view that these variables reach steady-state levels around the time of full leaf expansion. This view is valid for some species, including many herbaceous plants and some deciduous trees (Šesták, 1985). However, the present study clearly shows that this view does not always hold.

In most herbaceous species, Rd is very high in newly unfolded leaves and then decreases dramatically to an almost steady-state level until the completion of leaf area expansion (Šesták, 1985). However, the present species showed high Rd even at full leaf expansion. High Rd in the early stages of leaf development is attributed to the metabolism associated with the 'construction' of new leaf tissue (Amthor, 1989). Therefore, a high rate of dark respiration at the completion of leaf expansion indicates that leaf construction is still underway. This result is consistent with the marked increase in  $P_N$  max, LMA and LNa at this stage.

In the six species studied, LN<sub>m</sub> was highest at the earliest stage of leaf expansion, and decreased sharply to the steady-state level. For delayed greening species from a tropical rainforest (Kursar and Coley 1991), the steady-state value of LN<sub>m</sub> was  $1.56 \pm 0.26\%$  (mean  $\pm$  s.d. of three species), similar to the value found in the present study. However, the delayed greening, tropical rainforest species, *Xylopia micrantha* and *Connarus panamensis*, showed very low LN<sub>m</sub> values even at the early stage of leaf expansion and LN<sub>m</sub> remained almost constant throughout leaf development (Kursar and Coley, 1991). In the present study, LN<sub>m</sub> was initially much greater than at the steady-state level. Low LN<sub>m</sub> in the early stages of leaf development may be a unique characteristic of delayed greening species against the high herbivory pressure in a tropical rainforest.

Leaf nitrogen content on an area basis is well correlated with the maximum photosynthetic rate on an area basis (Evans, 1989). Given that 75 to 80% of leaf nitrogen is in the chloroplasts (data for pea leaves, Makino and Osmond, 1991), the strong relationship can be understood. In the present study, NUE was low in all six species when the leaves were young (Fig. 3). Low NUE in developing leaves might be caused by several factors. First, at early stage of

*panamensis* (Rob.) Saff. (Kursar and Coley, 1992b); *Ma*, *Morisonia americana* L. (Sobrado, 1991, 1992); *Ol*, *Ouratea lucens* (H.B.K.) Engler in Mart. (Kursar and Coley, 1992b); *Pv*, *Phaseolus vulgaris* L. (Čatský, 1976); *Qr*, *Quercus rubra* L. (Hanson *et al.*, 1988); *Tc*, *Theobroma cacao* L. (Baker and Hardwick, 1973; Choong *et al.*, 1992); *Xm*, *Xylopia micrantha* Tr. & Planch. (Kursar and Coley, 1992b). □, ▽, and ■ indicate plants in which rate of net photosynthesis on an area basis ( $P_N$  max) peaks before, at or after full expansion, respectively. Correlation coefficients ( $r$ ) are given in each graph. \*\*\* $P < 0.01$ ; ns, not significant.

leaf expansion, intercellular air spaces in the mesophyll are poorly developed so that the high diffusion resistance to CO<sub>2</sub> from the ambient air to the sites of carboxylation may limit CO<sub>2</sub> assimilation considerably (Leech and Baker, 1983). Second, nitrogen in developing leaves may not be allocated to photosynthetic components, but rather to the respiratory enzymes to support the high respiration rate. An ultrastructural study of wheat actually revealed that mitochondria were numerous in young leaves (Tobin, 1992) this may also be true of woody species. These factors probably explain the extremely low NUE in the developing leaves of the species studied here.

#### *Leaf maturation period, expansion period and delayed period*

We found significant positive relationships between P<sub>N</sub> max, LNA and LMA in all six species (Fig. 4). Leaves are composed of various types of cells which show different growth patterns during leaf development (Maksymowych, 1973) so that changes in LMA during development of the leaf reflect complex features. However, a large proportion of dry mass in mature leaves of woody species is made up of cellulose, hemicellulose and lignin (Chapin, McKendrick and Johnson, 1986; Chapin, 1989), which are important components of cell walls. The strong correlation between P<sub>N</sub> max, LNA and LMA may, thus, suggest that the investment of nitrogen resources into leaves and, thereby, the increase in photosynthetic activity, occurs simultaneously with the construction of cell walls during leaf development.

The relationships between P<sub>N</sub> max, LNA and LMA during leaf development have also been found for a herbaceous species (cucumber, *Cucumis sativus* L.; Ho *et al.*, 1984), a deciduous tree (apple; Marini and Barden, 1981), a deciduous liana (kiwifruit, *Actinidia deliciosa* var. *deliciosa* L.; Buwalda *et al.*, 1991), a hardwood tree species (Jurik, 1986) and a xerophyte (*Morisonia americana* L.; Sobrado, 1992), although the authors of these papers did not point out this relationship explicitly. Thus, the relationships may hold across many plants with different life forms.

There are considerable variations in the steady-state LMA among plants, especially when species of different life forms are compared. Since leaves with larger steady-state LMAs require more resources for their construction, we expected that such leaves would develop slowly compared to leaves with smaller steady-state LMAs. We, therefore, hypothesized that the period from emergence to photosynthetic maturation of a leaf ('leaf maturation period') would depend on the steady-state LMA. Using the existing data of leaf development for other plant species across several life forms (for references, see the legend to Fig. 5), we estimated the 'maturation period' of the leaves of these species. Plotting these data together with the present data against steady-state LMA revealed a significant positive relationship, which strongly supports our hypothesis (Fig. 5A). In contrast, the period from bud break to full expansion showed no significant correlation with steady-state LMA (Fig. 5B). We also calculated the period from full leaf expansion to photosynthetic maturity, the 'delayed period'.

There was a significant correlation between delayed period and steady-state LMA (Fig. 5C). Since leaf expansion period did not vary greatly among species, the large variation in delayed period was mainly due to variation in maturation period.

The steady-state LMA of the *C. sieboldii* tree in the shade (indicated as Cs\*) was smaller than that of the leaves in the sun. In other words, such shade leaves need less resources. As we expected, the leaf maturation and delayed periods of shade leaves were shorter than those of leaves in the sun (Fig. 5A and C). Although the maturation periods of *Xylopia micrantha* and *Desmopsis panamensis*, delayed greening species reported by Kursar and Coley (1992b), were somewhat longer than the other species with similar steady-state LMAs, the deviation was not marked. Therefore, the trends shown in Fig. 5 may be quite general across leaves of many species.

The present study revealed some general trends of leaf development. These can be summarized as follows: (1) the investment of nitrogen into leaves occurs in parallel with the investment of carbon for leaf structure; (2) species with large steady-state LMAs tend to have long maturation periods; (3) the leaf expansion period is less variable than the leaf maturation period. In many species with large steady-state LMA, greening or photosynthetic maturation and the increase in LMA are completed well after full leaf expansion. These general trends would comprehensively explain the 'delayed greening' in various species including the delayed greening species from tropical rainforests reported by Kursar and Coley (1992b).

#### ACKNOWLEDGEMENTS

We are grateful to Dr T. Koike for helpful suggestions and encouragement. We also thank Drs M. Ohsawa, I. Ikusima, T. Tsuchiya, T. Yabe, and D. R. Bhujju and Mr T. Shumiya for continuous encouragement. Dr Y. T. Hanba is thanked for conducting nitrogen analysis. Drs A. Takenaka, Y. T. Hanba, K. Noguchi and S. Funayama and Mr H. Muraoka are thanked for reading an earlier draft. We thank staff members of University Forests of the University of Tokyo for their kind support.

#### LITERATURE CITED

- Amthor JS.** 1989. *Respiration and crop productivity*. Berlin: Springer-Verlag.
- Baker NR, Hardwick K.** 1973. Biochemical and physiological aspects of leaf development in cacao (*Theobroma cacao*). I. Development of chlorophyll and photosynthetic activity. *New Phytologist* **72**: 1315–1324.
- Buwalda JG, Meekings JS, Smith GS.** 1991. Seasonal changes in photosynthetic capacity of leaves of kiwifruit (*Actinidia deliciosa*) vines. *Physiologia Plantarum* **83**: 93–98.
- Čatský J, Tichá I, Solárová J.** 1976. Ontogenetic changes in the internal limitations to bean-leaf photosynthesis. *Photosynthetica* **10**: 394–402.
- Chapin III PS, McKendrick JD, Johnson DA.** 1986. Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth form: implications for herbivory. *Journal of Ecology* **74**: 707–731.
- Chapin III PS.** 1989. The cost of tundra plant structures: evaluation of concepts and currencies. *The American Naturalist* **133**: 1–19.

- Choong MF, Lucas PW, Ong JSY, Pereira B, Tan HTW, Turner IM. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist* 121: 597–610.
- Coley PD, Aide TM. 1991. A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forest. In: Price PW, Thomas M, Lewinsohn G, Fernandes GW, Benson WW, eds. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. New York: Wiley & Sons, 25–49.
- Coley PD, Kursar TA. 1997. Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological trade-offs. In: Mulkey SS, Chazdon RL, Smith AP, eds. *Tropical forest plant ecophysiology*. New York: Chapman & Hall, 305–336.
- Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of  $C_3$  plants. *Oecologia* 78: 9–19.
- Hanson PJ, Isebrands JG, Dickson RE, Dixon RK. 1988. Ontogenetic patterns of  $CO_2$  exchange of *Quercus rubra* L. leaves during three flushes of shoot growth I. Median flush leaves. *Forest Science* 34: 55–68.
- Ho LC, Hurd RG, Ludwig LJ, Shaw AF, Thornley JHM, Withers AC. 1984. Changes in photosynthesis, carbon budget and mineral content during the growth of the first leaf of cucumber. *Annals of Botany* 54: 87–101.
- Jensen CR, Mogensen VO, Mortensen G, Andersen MN, Schjoerring JK, Thage JH, Koribidis J. 1996. Leaf photosynthesis and drought adaptation in field-grown oilseed rape (*Brassica napus* L.). *Australian Journal of Plant Physiology* 23: 631–644.
- Jurik TW. 1986. Temporal and spatial patterns of specific leaf weight in successional hardwood tree species. *American Journal of Botany* 73: 1083–1092.
- Koike T. 1986. A method for measuring photosynthesis with detached parts of deciduous broad-leaved trees in Hokkaido. *Journal of Japanese Forestry Society* 68: 425–428.
- Koike T. 1990. Autumn coloring, photosynthetic performance and leaf development of deciduous broad-leaved trees in relation to forest succession. *Tree Physiology* 7: 21–32.
- Kursar TA, Coley PD. 1991. Nitrogen content and expansion rate of young leaves of rain forest species: implications for herbivory. *Biotropica* 23: 141–150.
- Kursar TA, Coley PD. 1992a. Delayed greening in tropical leaves: an anti-herbivore defense? *Biotropica* 24: 256–262.
- Kursar TA, Coley PD. 1992b. Delayed development of the photosynthetic apparatus in tropical rainforest species. *Functional Ecology* 6: 411–422.
- Kursar TA, Coley PD. 1992c. The consequences of delayed greening during leaf development for light absorption and light use efficiency. *Plant, Cell and Environment* 15: 901–909.
- Lee DW, Brammeier S, Smith AP. 1987. The selective advantages of anthocyanins in developing leaves of mango and cacao. *Biotropica* 19: 40–49.
- Leech RM, Baker NR. 1983. The development of photosynthetic capacity in leaves. In: Dale JE, Milthorpe FL, eds. *The growth and functioning of leaves*. Cambridge: Cambridge University Press, 271–307.
- Maksymowych R. 1973. Analysis of leaf development. In: Abercrombie M, Newth DR, Torrey JG, eds. *Developmental and cell biology*. Cambridge: Cambridge University Press, 50–58.
- Makino A, Osmond B. 1991. Effects of nitrogen nutrition on nitrogen partitioning between chloroplasts and mitochondria in pea and wheat. *Plant Physiology* 96: 355–362.
- Marini RP, Barden JA. 1981. Seasonal correlations of specific leaf weight to net photosynthesis and dark respiration of apple leaves. *Photosynthesis Research* 2: 251–258.
- Šesták Z. 1985. *Photosynthesis during leaf development*. The Hague: Dr W. Junk.
- Sobrado MA. 1991. Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. *Functional Ecology* 5: 608–616.
- Sobrado MA. 1992. The relationship between nitrogen and photosynthesis in relation to leaf age in a tropical xerophytic tree. *Photosynthetica* 26: 445–448.
- Tobin AK. 1992. *Plant organelles compartmentation of metabolism in photosynthetic cells*. Cambridge: Cambridge University Press, 293–323.
- Yamaguchi T, Friend DJC. 1979. Effect of leaf age and irradiance on photosynthesis of *Coffea arabia*. *Photosynthetica* 13: 271–279.