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Acclimation of leaf characteristics of *Fagus* species to previous-year and current-year solar irradiances

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Summary To examine the effects of different solar irradiances on leaf characteristics at the leaf primordium and expansion stages, we shaded parts of branches in the upper canopies of two adult beech trees, *Fagus crenata* Blume and *Fagus japonica* Maxim., for 4 years. The treatments during the leaf primordium and leaf expansion stages, respectively, were: (1) high light and high light (H, control), (2) high light and low light (HL), (3) low light and low light (LL), and (4) low light and high light (LH). Both number of cell layers in palisade tissue and individual leaf area were affected by the previous-year irradiance, whereas cell length of palisade tissue was larger in LH leaves than in LL leaves, suggesting determination by current-year irradiance. Lamina chlorophyll/nitrogen ratio was higher in HL and LL leaves than in LH leaves, suggesting determination by current-year irradiance. Diurnal minimum values of leaf water potential measured under sunlit conditions were lower in H and LH leaves than in HL and LL leaves. Effective osmotic adjustment was found in H and LH leaves, suggesting that leaf water relations were affected by current-year irradiance. Net photosynthetic rate and stomatal conductance measured under sunlight conditions were higher in H and LH leaves than in HL and LL leaves. Thus, effects of current-year irradiance had a greater effect on leaf-area-based daily carbon gain than previous-year irradiance.

Keywords: canopy shading experiment, chlorophyll, Fagus species, light acclimation, nitrogen, photosynthesis, water relations.

Introduction

Changes in solar irradiance usually cause changes in photosynthetic properties among canopy leaves. This acclimation is especially important in trees that have a large light gradient within the canopy (e.g., Ackerly and Bazzaz 1995, Ishida et al. 1999*a*) and in leaves that are likely to encounter various light environments throughout long life spans (Schoettle and Smith 1991, Ishida et al. 1999*c*). These variations may allow a tree to maximize total carbon gain at the whole-canopy level (Hirose and Werger 1987, Ellsworth and Reich 1993, Evans 1993*a*, 1993*b*, Hollinger 1996).

Fagus crenata Blume and *Fagus japonica* Maxim. are winter-deciduous tree species, in which leaf expansion and shoot elongation are completed in a single flush in spring. Such species form leaf and shoot primordia in winter buds during the previous year (Kozlowski and Clausen 1966, Eschrich et al. 1989, Kimura et al. 1998). This pattern of shoot and leaf development suggests a limited capacity to acclimate to changing light environments in response to canopy gap opening or closure after bud formation. To determine how leaves of these trees acclimate to light, it is necessary to examine not only the effects of current-year light environment, but also the effects of previous-year light environment.

Water use of plants is sometimes coupled with stomatal behavior and net photosynthetic rate (P_n) (Ryan and Yoder 1997). During daytime, when sun-exposed leaves experience a high transpirational demand, stomata may close to maintain leaf turgor potential (e.g., Robichaux 1984, Ishida et al. 1992) and prevent cavitation in xylem tissue (e.g., Tyree and Sperry 1988, Tyree and Ewers 1991). Stomatal closure will sometimes limit the CO_2 supply to the leaf internal carboxylation sites, leading to a decrease in P_n (Ishida et al. 1999*b*). To maintain relatively high stomatal conductance and P_n under conditions of high transpiration demand, plants must either increase leaf-area-based hydraulic conductance or decrease leaf osmotic potentials (Turner and Jones 1980, Ishida et al. 1992, Gebre et al. 1998). We hypothesize that acclimation of photosynthetic properties to year-to-year changes in solar irradiance is affected by the degree of acclimation not only of leaf morphological and physiological properties, but also of leaf water relations.

To test this hypothesis, we determined (1) how various leaf morphological and physiological properties are affected by previous-year and current-year irradiances at the top of the canopy; and (2) how *in situ* diurnal carbon uptake of the top-canopy leaves is related to leaf morphology, physiology and leaf water relations. Adult trees of two winter-deciduous tree species, *F. crenata* and *F. japonica* were examined. To

distinguish between the effects of current-year and previous-year light conditions, we experimentally shaded parts of upper-canopy branches for four consecutive years to provide canopy leaves that formed under different irradiances during the leaf primordium and leaf expansion stages.

Materials and methods

Study site and plant materials

The study was conducted in a temperate deciduous forest at Nakoso, Fukushima, Japan (36°58′ N, 140°36′ E, altitude 700 m) from 1995 to 1998. Mean annual air temperature and precipitation during the 4-year experimental period were 9.5 °C and 1600 mm, respectively. We used a 15-m-tall tower to measure climatological and leaf ecophysiological traits in adjacent mature high-canopy trees of *F. crenata* and *F. japonica* (about 15 m tall and 100 years old). The tower is located at a ridge site with a thin leaf litter layer (about 3 cm) over a brown forest soil (Dydtric Cambisols). No severe soil-drying episodes occurred during the experimental period.

Climatological data at the top- (16 m) and lower-canopy (8 m) heights were continuously recorded with a data logger (Mes-901, Koito-Seisakusho Co., Tokyo, Japan) at 10-min intervals. The ratio of total daily photosynthetic photon flux density (PPFD) in the lower canopy relative to incident total daily PPFD just above the canopy (relative PPFD; rPPFD) was about 60% before leaf bud break and decreased during leaf expansion to about 7% by the end of May. Thereafter, rPPFD remained at a constant low value until leaf fall in mid-October.

Fagus crenata and *F. japonica* are winter-deciduous climax tree species of the single-flushing shoot type. During each year of the study, leaf expansion began in early May and each leaf took about 2 weeks to reach full expansion. The onset of leaf flush occurred about 1 week earlier in *F. japonica* than in *F. crenata*. Leaf physiological and morphological traits were measured in early August of each year.

In situ shading of upper-canopy branches

In April 1995 (before bud break), two shading frames (about 2 × 2 × 2 m) were fixed over the top parts of two upper-canopy branches bearing about 200 shoots that were exposed to full sunlight in previous years. The frames were covered with neutral shade-cloth to set the PPFD inside the frame equal to that at a canopy height of 8 m (about 5% rPPFD). Red/far-red ratio at midday, air temperature (T_{air}) and relative humidity (RH) did not differ significantly between the inside and outside of the shading frames. The shade-cloths were removed after leaf fall to avoid destruction by snow. The frames were covered with shade-cloth the following April, before bud break. Leaves on the same branch were examined during four consecutive years. The five treatments were: (1) leaves exposed to high light at the leaf primordium stage and low light at the leaf expanding stage in 1995 (HL), (2) leaves exposed to low light at both leaf primordium and leaf expanding stages in 1996 and 1997 (LL), (3) leaves exposed to low light at the leaf primordium stage and high light at the leaf expanding stage in 1998 (LH), (4) high-light leaves exposed to full sun at both the primordium and leaf expanding stages (H, control), and (5) low-light leaves maintained in shaded conditions in the lower canopy at a height of about 8 m (L).

Analysis of leaf anatomical and biochemical traits

Seven leaves per treatment were selected for determination of specific leaf area (SLA; the ratio of leaf area to dry mass) and lamina nitrogen (N) concentration. Leaves were dried at 80 °C for 48 h to obtain leaf dry mass. Dried leaves were broken into pieces, and about 50 mg of dried lamina tissue was used for the analysis of N concentration. Lamina N concentrations were measured by the Kjeldahl method.

Five leaves per treatment were analyzed for lamina chlorophyll (Chl) and lamina anatomical properties. To determine lamina Chl a and b concentrations, leaf discs were obtained with a borer (10 cm^2) from each fresh leaf and homogenized in cold 80% (v/v) acetone. Leaf homogenates were centrifuged at 10,000 *g* for 10 min at 4 °C. Chlorophyll concentrations were determined spectrophotometrically (Ubest-30, Japan Spectroscopic Co., Tokyo, Japan), following the procedure of Arnon (1949). Lamina cross sections were cut with a revolving microtome (MT-2, NKsystem Co. Ltd., Osaka, Japan) at 10 µm thickness. The thicknesses of the lamina, epidermal layer, palisade mesophyll layer, and spongy mesophyll layer in each leaf were measured with the aid of a light microscope. Annual changes in individual leaf area were determined for 100 randomly selected canopy leaves per treatment. Annual changes in stomatal density were determined on five randomly selected leaves per treatment by obtaining a replica of each leaf surface with a celluloid plate (Universal Micro-printing, SUMP, Tokyo, Japan).

Diurnal changes in microclimate, leaf gas exchange and leaf water potential

Microclimate data (PPFD, T_{air}, RH and wind speed) were stored every minute in a data logger. Leaf temperature (T_{leaf}) was measured with fine-wire copper constantan thermocouples (diameter 0.1 mm, Hayashi-Denko Co., Tokyo, Japan) attached to the abaxial leaf surface by adhesive tape. Leaf temperature was used to calculate leaf-to-air vapor pressure deficit (ΔW).

Measurements of diurnal leaf gas exchange were conducted in H, HL, LH and LL leaves in full sunlight by removing the shade cloths in early August. Five leaves were selected, and the diurnal measurements were conducted approximately every 90 min from predawn to dusk. Diurnal changes in net photosynthesis rate (P_n, µmol m^{-2} s^{-1}) and water vapor stomatal conductance (g_s, mmol m^{-2} s^{-1}) per unit leaf area were measured *in situ* with a portable H_2O/CO_2 analyzer (LCA-4, ADC Co., Hoddesdon, U.K.) in an open system. Transpiration rate (E, mmol m^{-2} s^{-1}) was determined as:

$$E = \Delta W\left(\frac{g_s g_b}{g_s + g_b}\right), \quad (1)$$

where g_b is boundary layer conductance (mmol m^{-2} s^{-1}), determined as (Jones 1992, Pearcy et al. 1989):

$$g_b = 0.446\left(0.715\left(\frac{\mu}{d}\right)^{0.5}\right)\left(\frac{273}{T_{leaf}}+273\right)\left(\frac{P}{101.3}\right)10^3, \quad (2)$$

where μ is wind speed (m s^{-1}) simultaneously measured with an anemometer (Model 6511, Kanomax Inc., Osaka, Japan), d is leaf length (m), and P is air pressure (kPa). Leaf water potential (Ψ_L, MPa) was also measured in the field with a pressure chamber (Model-3000, SoilMoisture Equipment Co., Santa Barbara, CA) at about 1-h intervals.

Measurements of leaf water relations

Assuming a steady-state water flow within the soil-plant-air continuum, leaf-area-based hydraulic conductance was determined from the slope of the relationship between area-based transpiration rate and leaf water potential. Predawn Ψ_L (about −0.15 MPa at a canopy height of 15 m) was used as a measure of soil water potential. There were no differences between predawn Ψ_L values of leaves enclosed overnight in plastic bags to minimize water loss and predawn Ψ_L values of leaves *in situ* (data not shown), indicating that soil water potential was equal to predawn Ψ_L in early summer.

To determine leaf water potentials at full turgor, leaf water potentials at the turgor loss point, and bulk modulus of elasticity in cell walls, pressure-volume (P-V) curves were constructed for three leaves per treatment. The selected shoots were fully rehydrated under dim light and moist conditions overnight. Measurement of Ψ_L was conducted stepwise with natural dehydration, according to Ishida et al. (1992). Maximum bulk modulus of elasticity in leaf cell walls (ε_{max}) was determined by linear regression between turgor potential and the free water content at the point of the steepest slope. Diurnal turgor potentials (Ψ_p) of leaves were estimated from the diurnal leaf water potentials (Ψ_L) and P-V curves.

Statistical analysis

To compare the range of acclimation in HL, LL, and LH leaves, a *t*-test was made between the HL, LL and LH leaves and H or L leaves, and between H and L leaves. Differences were judged to be significant at $P < 0.05$.

Results

Effects of solar irradiance on leaf properties

Differences in individual leaf area for *F. crenata* and *F. japonica* are shown in Figures 1A and 1B. Leaf area was significantly larger in L leaves than in H leaves. In both species, leaf areas of HL leaves were similar to those of H leaves. For *F. crenata*, the leaf areas of LL and LH leaves were similar or larger than those of L leaves. In contrast, for *F. japonica*, the leaf area of LH leaves was not significantly different from that of L leaves. These data suggest that irradiance in the previous year had a strong effect on individual leaf area in *F. crenata*, but only a weak effect in *F. japonica*. Among study years, H leaves of *F. japonica* had the smallest leaf area in 1995, probably because 1995 was a mast year for seeds.

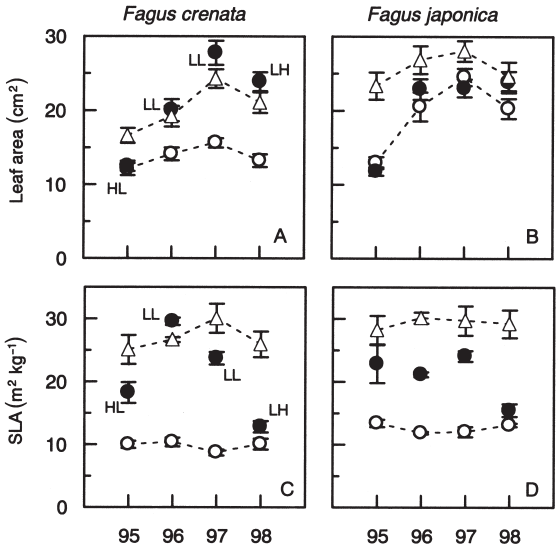

Figure 1. Annual changes in leaf area (A, B) and specific leaf area (SLA; C, D) in individual leaves of *F. crenata* (A, C) and *F. japonica* (B, D). Symbols: (○) H; (△) L; and (●) shaded leaves. Shaded leaves were: HL leaves in 1995; LL leaves in 1996 and 1997; and LH leaves in 1998. Vertical bars represent 95% confidence intervals.

In both species, irradiance in the previous year affected SLA (Figures 1C and 1D), mainly because of the effects of previous-year irradiance on leaf anatomical properties such as the number of cell layers. For *F. crenata*, the palisade tissue of H and HL leaves had two layers, whereas it comprised one cell layer in LL, LH, and L leaves (Figures 2A, 2C, 2E and 2G; data for LH leaves not shown). This finding indicates that *F. crenata* cannot change the number of palisade cell layers in response to current-year irradiance. For *F. japonica*, the palisade tissue of leaves in all treatments consisted of only one cell layer, even in H leaves (Figures 2B, 2D, 2F and 2H).

Lamina thickness of HL and LH leaves of *F. crenata* was intermediate between that of H and L leaves, whereas there was no significant difference in lamina thickness between HL and L, or between LH and H leaves of *F. japonica* (Figure 3). The difference between species in the adjustment of lamina thickness to irradiance was a result of a difference in the effect of previous-year irradiance on the number of palisade cell layers. Both species were able to change individual cell lengths according to the light conditions prevailing during leaf development.

Lamina mass-based N and Chl concentrations and Chl/N ratio were significantly lower in H leaves than in L leaves of both species (Figure 4). Lamina N concentrations of H leaves were 10–17% lower than those of L leaves, and Chl concentrations of H leaves were 47–57% lower than those of L leaves. The Chl a/b ratio was significantly higher in H leaves than in L leaves. The N and Chl concentrations, Chl/N ratio, and Chl a/b ratio in HL and LL leaves were close to the values for L leaves,

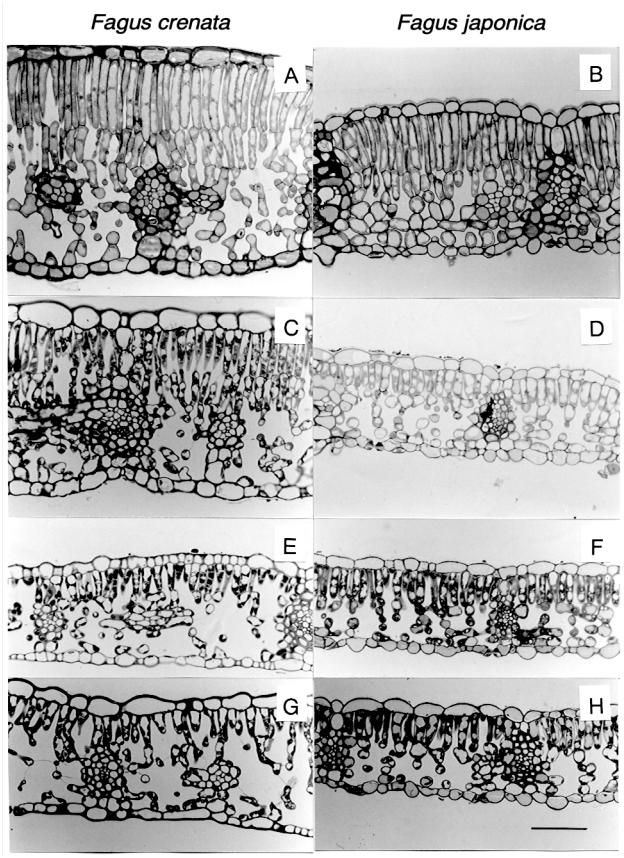

Figure 2. Micrographs of transverse sections of leaves of *F. crenata* (A, C, E, G) and *F. japonica* (B, D, F, H). The bar indicates 50 µm. The H (A, B), HL (C, D) and L (G, H) leaves were collected in 1995, and the LL (E, F) leaves were collected in 1996.

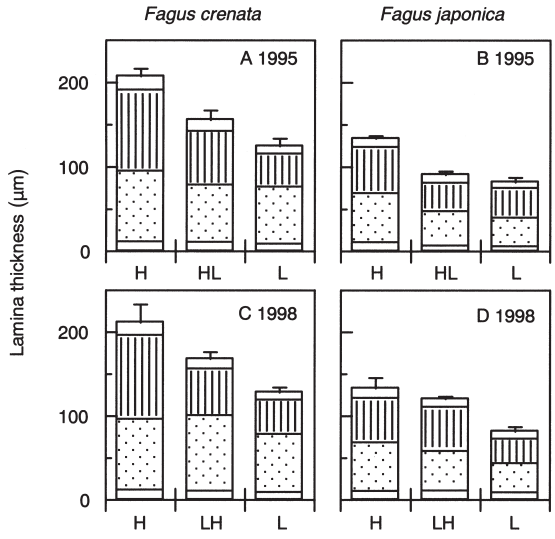

Figure 3. Lamina thickness in 1995 in H, L and HL leaves (A, B) and in 1998 in H, L, and LH leaves (C, D) of *F. crenata* (A, C) and *F. japonica* (B, D). The four areas in the bars represent (from top to bottom) thickness of upper epidermal layer, palisade mesophyll layer, spongy mesophyll layer, and under epidermal layer. Vertical bars represent 95% confidence interval of lamina thickness.

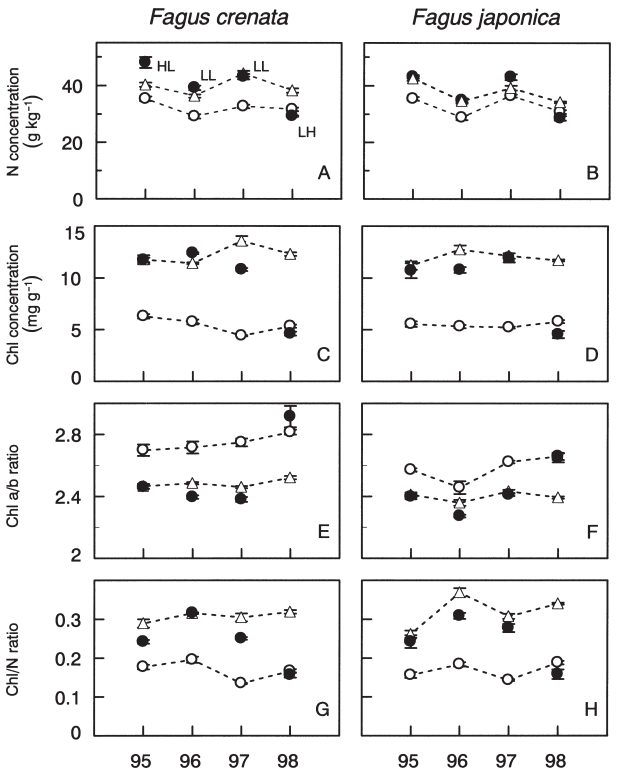

Figure 4. Changes in N concentration (A, B), Chl concentration (C, D), Chl a/b ratio (E, F) and Chl/N ratio (G, H) for *F. crenata* (A, C, E, G) and *F. japonica* (B, D, F, H). Symbols: (○) H; (△) L; and (●) shaded leaves. Shaded leaves were: HL in 1995; LL in 1996 and 1997; and LH in 1998. Vertical bars represent ± 1 SE.

whereas these characteristics in LH leaves were close to those in H leaves. Thus, lamina N and Chl were strongly affected by current-year irradiance during leaf development.

Effects of irradiance on leaf gas exchange

For both species, P_n and g_s were affected by current-year light conditions. Diurnal P_n measured under saturating light conditions (> 500 µmol m^{-2} s^{-1} PPFD) was significantly lower in LH, HL and LL leaves than in H leaves (Table 1). Differences in P_n between H and LL leaves were larger in *F. crenata* than in *F. japonica*. For both species, P_n and g_s were higher in LH leaves than in HL and LL leaves. Net photosynthetic rate in HL leaves was about 43% lower than in H leaves, and g_s in HL leaves was about 35–46% lower than in H leaves. Because stomatal density of HL leaves was not significantly less than that of H leaves (mean ± SD; 230 ± 41 cm^{-2} in HL and 226 ± 26 cm^{-2} in H for *F. crenata*), the variation in g_s between HL and H leaves was attributed to stomatal apparatus rather than to stomatal density. For both species, P_n was 21–31% lower in LH leaves than in H leaves, and g_s was 4–11% lower in LH leaves than in H leaves. Thus, the values of P_n and g_s were affected by the current-year light ennvironment.

The slope of the linear regression between absolute values of Ψ_L and E provided an estimate of hydraulic resistance per

Table 1. Net photosynthetic rate (P_n, μmol m^{-2} s^{-1}) and water vapor stomatal conductance (g_s, mmol m^{-2} s^{-1}) under sunlit conditions in shading experiment leaves for *F. crenata* and *F. japonica*. Data were obtained at a PPFD of more than 500 μmol m^{-2} s^{-1}, and are presented as means ± 1 SD. Values in parenthesis represent the percentage of values for H in each year.

		HL	LL in 1996	LL in 1997	LH
F. crenata	P_n	4.33 ± 1.45 (56.6)	2.07 ± 0.83 (28.8)	3.61 ± 2.00 (42.5)	7.63 ± 1.28 (79.1)
	g_s	68.2 ± 13.9 (53.6)	65.5 ± 15.2 (51.0)	77.3 ± 18.6 (56.4)	166.9 ± 17.0 (88.7)
F. japonica	P_n	3.05 ± 1.66 (56.5)	1.85 ± 0.64 (32.6)	3.22 ± 1.65 (46.8)	4.76 ± 0.78 (69.4)
	g_s	55.3 ± 23.4 (65.1)	53.6 ± 22.4 (54.4)	69.9 ± 25.8 (67.1)	130.4 ± 13.6 (95.6)

unit leaf area (Figure 5). There was no significant difference between the linear regressions for H and HL leaves in either species (P = 0.391 for *F. crenata* and 0.301 for *F. japonica*), indicating that the shading treatments had no effect on soil-to-leaf hydraulic resistance.

Leaf water relations, such as osmotic potential at full turgor (Ψ_π^0) and leaf water potential at the turgor loss point (Ψ_L^{tlp}), were determined in response to the current-year irradiance (Table 2). In both species, Ψ_π^0 was significantly higher in HL and LL leaves than in H leaves, and Ψ_π^0 in LH leaves was similar to or less than that in H leaves. Leaf water potential at the turgor loss point was significantly higher in HL and LL leaves than in H leaves, and similar in LH and H leaves. The shading treatments had no effect on maximum bulk modulus of elasticity in cell walls (ε_{max}). The diurnal minimum value of the leaf water potential (Ψ_L^{min}) in HL and LL leaves was higher than in H leaves. Thus, the degree of osmotic adjustment and daily Ψ_L^{min} were mainly dependent on solar irradiance in the current year. We compared the coefficient of variation (CV) for Ψ_L^{min} and the daily minimum values in turgor potential (Ψ_p^{min}) among all shaded leaves. The CVs for Ψ_L^{min} (0.323 in *F. crenata* and 0.166 in *F. japonica*) were larger than those for Ψ_p^{min} (0.018 and 0.133, respectively), indicating that Ψ_p^{min} was relatively stable among leaves in all treatments.

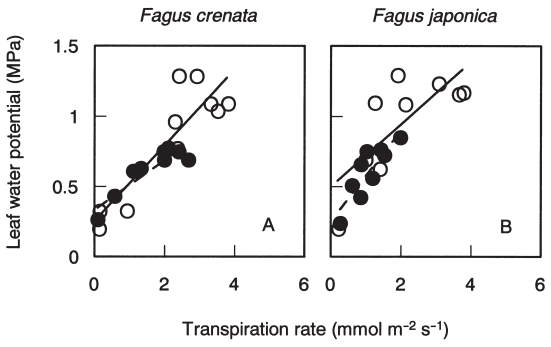

Figure 5. Relationship between absolute values of diurnal leaf water potentials (Ψ_L) and transpiration rate in (○) H and (●) HL leaves of *F. crenata* (A) and *F. japonica* (B) in 1995.

Discussion

Effects of solar irradiance on leaf characteristics

Effects of previous-year light environment on leaf anatomical traits differed between the two *Fagus* species, even though both species have the single-flush type of leaf phenology. The single palisade cell layer in *F. japonica* leaves was mainly determined by current-year PPFD, which is consistent with results of previous studies of *F. japonica* (Kimura et al. 1998) and *Acer tenuifolium* Koidz. (Koike et al. 1997). In contrast, the leaf properties in *F. crenata* were affected by both previous-year and current-year PPFDs, as previously observed in *Fagus sylvatica* L. (Eschrich et al. 1989, Tognetti et al. 1998). Sun leaves of *F. crenata* and *F. sylvatica* were unable to change the number of cell layers in palisade tissue in response to the current-year PPFD, indicating that cell divisions are completed before bud break and were determined by irradiance at the bud formation stage (i.e., the previous-year irradiance) (Eschrich et al. 1989, Koike et al. 1997). In an ivy (*Hedera helix* L.), even mature leaves can change the number of cell layers in the palisade parenchyma in response to current-year irradiance (Bauer and Thoni 1988). Because the lengths of individual cells changed in response to changes in PPFD at the leaf development stage, the change in leaf thickness in response to year-to-year changes in PPFD was faster in *F. japonica* than in *F. crenata*. We conclude that the acclimation potential in leaf morphology was more restricted in plants with several cell layers in the palisade parenchyma than in plants with a single cell layer in the palisade parenchyma.

Although leaf properties were related to previous-year and current-year irradiance, they were probably not related to sink effects of carbohydrate reserves in trunks. In both species, LL leaves had similar properties to L leaves located at a similar rPPFD. Kimura et al. (1998) found that, in *F. japonica*, the properties of shoots produced in a shade frame were similar to the properties of shoots receiving a similar rPPFD within the canopy. These findings indicate that branches are fairly independent or autonomous with respect to their carbon economy (Sprugel et al. 1991) and that sink effects are minor.

Biochemical properties such as lamina N and Chl concentrations adjusted in response to the light intensity at the leaf

Table 2. Effects of shading on leaf water relations for *F. crenata* and *F. japonica*. Leaf properties in the shading experiment (HL, LL in 1996 and 1997, and LH) were compared with the 4-year average for H. Within a species, the Student's *t*-test was used to detect significant differences (** = $P < 0.001$; * = $P < 0.05$; ns = not significant).

	Control	Shading experiment leaves			
	H	HL	LL	LL	LH
F. crenata					
Osmotic potential at full turgor (MPa)	–2.14	–1.45**	–1.18**	–1.55**	–2.13 ns
Water potential at turgor loss point (MPa)	–2.57	–1.88**	–1.63**	–1.76**	–2.58 ns
Bulk modulus of elasticity in cell walls (MPa)	33.4	16.3*	15.5*	30.8 ns	24.3 ns
Diurnal minimum water potential (MPa)	–1.3	–0.8	–0.6	–0.8	–1.6
Diurnal minimum turgor potential (MPa)	1.1	0.8	0.7	0.8	0.8
F. japonica					
Osmotic potential at full turgor (MPa)	–1.96	–1.68**	–1.67**	–1.54**	–2.11*
Water potential at turgor loss point (MPa)	–2.46	–2.22*	–2.30*	–2.00**	–2.58 ns
Bulk modulus of elasticity in cell walls (MPa)	19.3	18.1 ns	16.0*	20.4 ns	22.2*
Diurnal minimum water potential (MPa)	–1.3	–0.9	–0.9	–1.0	–1.2
Diurnal minimum turgor potential (MPa)	0.9	0.8	0.8	0.7	1.0

development stage. Shaded leaves had a higher Chl/N ratio and a lower Chl a/b ratio than sunlit leaves, indicating that N in the shaded leaves could be preferentially allocated to the light-harvesting components (chlorophyll proteins) rather than to the carbon-fixation components (Rubisco and electron transport proteins) (Terashima and Evans 1988, Evans 1989). Our results indicate that mass-based N and Chl concentrations and N rearrangements within a leaf could be substantially adjusted to the current-year light environment.

In situ leaf gas exchange

Stomatal opening is frequently enhanced by increasing soil-to-leaf hydraulic conductance to promote water uptake, or by making osmotic adjustments to maintain leaf or turgor potentials (e.g., Ishida et al. 1992, Hubbard et al. 1999). We found that soil-to-leaf hydraulic conductance was not affected by previous-year irradiance in either *Fagus* species. Therefore, we attributed stomatal opening, which was dependent on current-year irradiance, to osmotic adjustment. The lower CV in Ψ_p^{min} than in Ψ_L^{min} supported the hypothesis that osmotic adjustment is an adaptive mechanism for maintaining Ψ_p (Turner and Jones 1980, Robichaux 1984). It has been suggested that leaves with large ε_{max} (rigid cell walls) can rapidly decrease Ψ_L by slight leaf dehydration without direct energy consumption (Salleo 1983, Ishida et al. 1992). Although there was no obvious treatment effect on ε_{max}, both Ψ_π^0 and Ψ_L^{tlp} were substantially determined by current-year irradiance. These data suggest that the effects of current-year irradiance on *in situ* diurnal carbon gain were larger than those of previous-year irradiance, despite a year-to-year time lag in acclimation of leaf morphology, especially in *F. crenata* trees with several cell layers in the leaf palisade tissue. Because of the complexity of hydraulic architecture and the variation in leaf specific conductivity in a crown (Tyree and Ewers 1991), more work is need to clarify the interactive effects of light quality and light quantity within the canopy and water relations on leaf carbon gain processes.

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