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The influence of previous irradiance on photosynthetic induction in three species grown in the gap and understory of a *Fagus crenata* forest

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Abstract

Photosynthetic induction responses to a sudden increase in photosynthetic photon flux density (PPFD) from lower background PPFD (0, 25, 50, and 100 μmol m^{-2} s^{-1}) to 1 000 μmol m^{-2} s^{-1} were measured in leaves of *Fagus crenata*, *Acer rufinerve* Siebold & Zucc., and *Viburnum furcatum* growing in a gap and understory of a *F. crenata* forest in the Naeba mountains. In the gap, *A. rufinerve* exhibited more than 1.2-fold higher maximum net photosynthetic rate (P_{Nmax}) than *F. crenata* and *V. furcatum*. Meanwhile, in the understory *F. crenata* exhibited the highest P_{Nmax} among the three species. The photosynthetic induction period required to reach P_{Nmax} was 3-41 min. The photosynthetic responses to increase in PPFD depended on the background PPFD before increase in PPFD. The induction period required to reach P_{Nmax} was 2.5-6.5-fold longer when PPFD increased from darkness than when PPFD increased from 100 μmol m^{-2} s^{-1}. The induction period was correlated with initial P_N and stomatal conductance (g_s) relative to maximum values before increase in PPFD. The relationship was similar between the gap and the understory. As the background PPFD increased, the initial P_N and g_s increased, indicating that the degrees of biochemical and stomata limitations to dynamic photosynthetic performance decreased. Therefore, photosynthetic induction responses to increase in PPFD became faster with the increasing background PPFD. The differences in time required to reach induction between species, as well as between gap and understory, were mainly due to the varying of relative initial induction states in P_N and g_s at the same background PPFD.

Additional key words: *Acer rufinerve*; *Fagus crenata*; photosynthetic photon flux density; photosynthetic induction; stomatal conductance; *Viburnum furcatum*.

Introduction

Plants growing on the forest floor are exposed to fluctuations in PPFD because of the presence of sunflecks. On a tropical rain forest floor, integrated PPFD per day in the understory and in a 400 m^2 gap were 1-2 and 20-35 %, respectively, of that above canopy (Chazdon and Fetcher 1984). In a light-limited environment like this, saplings need to capture photons efficiently. A higher radiant energy-use efficiency, if it exists, may be attributed either to a faster induction responses to increase in PPFD or higher net photosynthetic rates (P_N) under constant irradiation. Poorter and Oberbauer (1993) described that a climax species of saplings grown in shady sites had faster rates of induction than saplings grown in bright sites with no difference in photon-saturated photosynthetic rate. A pioneer species of saplings grown in bright sites had higher photon-saturated P_N than saplings grown in shady sites with no difference in the rates of induction.

Photosynthetic acclimation to a changing irradiance has been studied on steady-state responses to radiation in different species (Chazdon 1986, Kitajima 1994, Chen and Klinka 1997, Murchie and Horton 1997, Gamper *et al.* 2000, Sailaja and Rama Das 2000). In general, leaves have a lower dark respiration rate (R_D) and a lower maximum net photosynthetic rate (P_{Nmax}) on a leaf area basis in the understory than in the gap. However, at low PPFDs, leaves have higher P_N and use low PPFD more efficiently in the understory than in the gap. The steady-state conditions applied in measurements of leaf photosynthesis do not hold under these transient sunflecks. Therefore dynamic photosynthetic responses under natural irradiance are not well understood. There have been studies of the dynamic photosynthetic response in different species (Chazdon and Pearcy 1986a, Pons *et al.* 1992, Kursar and Coley 1993, Poorter and Oberbauer 1993, Chen and Klinka 1997, Valladares *et al.* 1997, Han *et al.* 1999). The induction state of the photosynthetic apparatus is dependent on the capacity for RuBP regeneration (Sassenrath-Cole and Pearcy 1992), the capacity

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for ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO)-catalysed carboxylation (Seemann *et al.* 1988), and g_s (Tinoco-Ojanguren and Pearcy 1992). Measurements of dynamic photosynthetic responses in controlled laboratory conditions have indicated that radiant energy-use efficiencies during sunflecks are greater in shade plants than in sun plants because of faster photosynthetic induction and greater post-irradiation assimilation in shade plants (Chazdon and Pearcy 1986b, Pons and Pearcy 1992, Tang *et al.* 1994). In addition, there have also been few studies on the effects of previous irradiation history on the photosynthetic induction response (Valladares *et al.* 1997, Han *et al.* 1999).

Fagus crenata Blume (Japanese beech), a late-successional and climax species, is ecologically the most important forest tree species in the cool-temperate natural forests of the mountainous zones in Japan (Ishizuka 1974). It is moderately shade tolerant and capable of regenerating under its own canopy. With decreasing photon availability, its specific leaf area increases and its R_D decreases (Liang *et al.* 1995). These changes are likely to make saplings more efficient in capturing photons in a light-limiting environment. *Acer rufinerve* Siebold & Zucc., a tree species that prefers sunny and moist places, often forms the sub-canopy in *F. crenata* forests (Karizumi 1979). *Viburnum furcatum*, a sub-tree species, often exists in the *F. crenata* forest (Makino 1961).

The objectives of this study were: (*1*) to compare the three species in the gap and understory, and (*2*) to demonstrate the possible influences of background PPFD in the photosynthetic induction responses to increases in PPFD.

Materials and methods

Study site and plants: Measurements were conducted on seedlings growing in a gap or understory of the *F. crenata* forest at Naeba Mountain in Niigata Prefecture, Japan (36°51'N, 138°40'E, altitude 700 m), in August 1999. The climate is cool and temperate. Mean annual precipitation near the site is 1 778 mm, according to a 30-year record from 1967 to 1996 (Japanese Bureau of Meteorology). Naturally occurring seedlings (5-10-years-old, 50-100 cm tall) were selected for study in both the gap and the understory. Plants growing near the centre or southern side of the gap were chosen as gap samples. The gap site received direct solar irradiance for two consecutive hours from 10:30 to 12:30. Meanwhile, the understory site about 40 m from the gap site was covered by canopy.

Irradiance: PPFD was measured with quantum sensors (*IKS-25*, Koito, Japan) connected to a data logger (*MES-901*, Koito, Japan). These sensors were calibrated with a quantum sensor (*LI-COR*, Lincoln, NE, U.S.A.). Four sensors were placed in the gap and the understory on the forest floor. These sensors were mounted on the top of 2-m stakes (approximately) and carefully levelled. Measurements were taken at 10-s intervals.

Gas exchange measurements: Photosynthetic induction responses were measured with a *LI-6400* portable photosynthesis measurement system, with a 2×3 cm chamber and *6400-02B* LED lamp (*LI-COR*, Lincoln, NE, U.S.A.). Measurements were made at a temperature of 22 °C, relative humidity of 70 % (vapour pressure deficit 8.2 Pa kPa^{-1}), and CO_2 concentration of 350 μmol mol^{-1}. After about 1 h at low background PPFD, the irradiance was increased above the photosynthetic PPFD saturation threshold (1 000 μmol m^{-2} s^{-1}). The photosynthetic PPFD saturation thresholds were about 400 and 200 μmol m^{-2} s^{-1} in the gap and understory seedlings of all the studied species, respectively (values not shown). The four background PPFDs were 0, 25, 50, and 100 μmol m^{-2} s^{-1}. Measurements were made at about 2-s intervals. R_D, P_N at different background PPFDs (P_{N25}, P_{N50}, and P_{N100}), maximum net photosynthetic rate (P_{Nmax}), and initial and maximum stomatal conductances (g_{s0}, g_{s25}, g_{s50}, g_{s100}, and g_{smax}) were statistically compared. Times to 50, 90, and 100 % induction (T_{50}, T_{90}, and T_{100}) were calculated; *i.e.*, the length of time taken to achieve 50, 90, and 100 % of P_{Nmax} (Chazdon and Pearcy 1986a).

Photosynthetic responses to CO_2 concentration were measured for the studied species with a *HCM-1000* portable photosynthesis measurement system using the *1010-M* climatised measuring cuvette with the *1050-H* lighting unit (*H. Walz*, Effeltrich, Germany). Air of known CO_2 concentration was prepared by mixing (*GMA-2*, *H. Walz*) CO_2-free air with compressed CO_2 from a gas cylinder. Measurements were made under a constant temperature of 22 °C, relative humidity of 70 % (vapour pressure deficit of 8.2 Pa kPa^{-1}), and PPFD of 700 μmol m^{-2} s^{-1} above the photosynthetic PPFD-saturation threshold.

Results

Irradiance: Mean total PPFDs for 12-h (06:00-18:00) of nine typical sunny days were 13.5 mol m^{-2} (38.1 % of above canopy) in the gap and 1.9 mol m^{-2} (5.4 % of above canopy) in the understory (Table 1). The frequency of PPFD was different between the gap and the understory. In the gap, PPFD readings of 50-100 μmol m^{-2} s^{-1} were the most frequent (24.6 %), and the relative frequency of PPFD below 100 μmol m^{-2} s^{-1} was 61.3 %. In the understory, PPFD readings of 25-50 μmol m^{-2} s^{-1} were the most frequent (38.4 %), and the relative frequency of PPFD below 50 μmol m^{-2} s^{-1} was 73.0 %.

Table 1. Radiation environment. Total PPFD [mol m^{-2} s^{-1}] for 12-h (06:00-18:00) and relative frequency [μmol m^{-2} s^{-1}] of classified PPFD in gap and understory, based on readings taken four sensors at 10-s intervals. Means ± SD of typical nine sunny days.

		Gap	Understory
Total PPFD		13.5±3.2	1.9±0.3
Relative frequency [%]	0-25	18.5±4.4	34.6±10.2
	25-50	18.2±5.7	38.4±6.7
	50-100	24.6±4.1	22.4±7.8
	100-200	16.2±5.8	2.7±0.6
	200-400	4.1±1.4	1.3±0.4
	above 400	18.4±4.5	0.6±0.4

Gas exchange parameters under constant irradiation: In both species, P_{Nmax} was significantly lower in understory seedlings than in gap seedlings (Table 2). These trends were observed for P_{N25} and P_{N50} except P_{N25} in *V. furcatum*. However, there were no significant differences, and these value were similar. In *V. furcatum*, the mean P_{N25} value was higher in the understory than in the gap. P_{Nmax} was 1.9-, 2.8-, and 2.2-fold higher in the gap than in the understory in *F. crenata*, *A. rufinerve*, and *V. furcatum*, respectively. In the gap, *A. rufinerve* exhibited greater than 1.2-fold P_{Nmax} values than *F. crenata* and *V. furcatum*. Meanwhile, in the understory, *F. crenata* exhibited the highest P_{Nmax} values of the three species. In both species, the mean R_D was lower in understory seedlings than in gap seedlings. A significant difference in R_D between the gap and the understory was observed only for *F. crenata*.

In all the species, g_{smax} was about 1.5-fold higher in gap seedlings than in understory seedlings. In both the gap and the understory, *F. crenata* exhibited the highest g_{smax} values of the three species.

Time course of photosynthetic induction and the effect of previous PPFD on the induction: Representative time courses for photosynthetic induction in *F. crenata* are shown in Fig. 1. When PPFD was increased to 1 000

Table 2. Gas exchange parameters for leaves of the studied species. Dark respiration rate (R_D) [μmol m^{-2} s^{-1}], net photosynthetic rate (P_{N25}, P_{N50}, P_{N100}) [μmol m^{-2} s^{-1}], and stomatal conductance (g_{s0}, g_{s25}, g_{s50}, g_{s100}) [mmol m^{-2} s^{-1}] were obtained at background PPFD before increase in PPFD. Numbers indicate PPFD. Maximum P_N (P_{Nmax}) and maximum g_s (g_{smax}) were obtained at the end of high PPFD (1 000 μmol m^{-2} s^{-1}). Means for three leaves each from a different tree ± SD. *Different lowercase and uppercase letters* adjacent to a mean indicate a significant between the same species at two sites ($p<0.05$, Student's *t*-test) and between different species at the same site ($p<0.05$), respectively. Mean relative P_N to P_{Nmax} and g_s to g_{smax} ± SD are given in parentheses.

Parameter	*Fagus crenata*		*Acer rufinerve*		*Viburnum furcatum*	
	Gap	Understory	Gap	Understory	Gap	Understory
R_D	-0.46±0.06 a	-0.22±0.08 b	-0.35±0.09	-0.21±0.08	-0.40±0.20	-0.25±0.12
P_{N25}	1.19±0.23 (15.6±1.9)	1.04±0.07 (31.4±6.4)	1.33±0.05 A (17.0±1.3)	1.21±0.15 (40.9±5.0)	0.89±0.16 B (16.0±3.1)	1.18±0.14 (42.3±7.7)
P_{N50}	1.88±0.60 (29.4±2.5)	1.87± 0.08 (57.5±8.2)	2.54±0.45 (31.0±3.6)	1.85±0.08 (66.7±1.4)	2.31±0.48 (35.1±3.5)	1.84±0.24 (69.6±5.0)
P_{N100}	3.49±1.06 (57.1±4.2)	2.46±0.47 (72.6±3.6)	4.74±0.19 Aa (55.6±6.0)	2.10±0.26 b (81.9±8.8)	4.06±0.15 Ba (66.3±9.3)	2.25±0.38 b (81.8±5.2)
P_{Nmax}	6.61±1.51 Aa	3.41±0.70 Ab	8.05±1.40 Ba	2.83±0.37 Bb	5.98±0.75 Aa	2.84±0.69 b
g_{s0}	19.0±17.2 (10.0±7.8)	10.0±6.3 (9.9±7.1)	28.4±25.1 (14.7±12.6)	16.3±8.0 (13.9±6.7)	43.3±30.5 (33.4±12.3)	38.2±22.2 (47.2±36.0)
g_{s25}	50.9±34.6 (22.7±4.9)	55.1±28.6 (43.6±24.9)	48.9±19.2 (30.6±3.3)	56.9±13.7 (53.9±13.6)	43.3±20.3 (31.9±6.2)	53.2±10.6 (68.1±10.2)
g_{s50}	47.1±9.1 (29.7±3.1)	61.8±13.7 (54.8±14.3)	62.9±27.3 (45.1±7.8)	71.7±1.6 A (75.0±6.0)	83.2±40.5 (52.1±15.7)	61.0±4.1 B (82.4±3.9)
g_{s100}	103.1±58.4 (48.4±11.6)	95.1±0.1 A (74.5±7.8)	115.5±8.6 a (62.3±4.4)	63.9±12.2 Bb (71.0±13.5)	102.2±31.4 (78.8±28.1)	62.0±10.9 B (84.9±8.5)
g_{smax}	188.6±62.9 Aa	122.2±32.1 Ab	167.7±38.5) Aa	102.6±14.8 Ab	133.9±30.0 Ba	82.3±24.8 Bb

μmol m^{-2} s^{-1}, P_N and g_s increased, whereas intercellular CO_2 concentration (C_i) decreased. The time course of induction varied by a sigmoid increase in P_N when PPFD was increased from darkness (0 μmol m^{-2} s^{-1}). However, P_N values increased hyperbolically when PPFD was increased from 50 and 100 μmol m^{-2} s^{-1}. These responses were also observed for *A. rufinerve* and *V. furcatum*. The three species in the gap had already reached above 55 % of P_{Nmax} at 100 μmol m^{-2} s^{-1}, whereas the three species in the understory had already reached above 57 % of P_{Nmax} at 50 μmol m^{-2} s^{-1} (Table 2).

The photosynthetic responses of leaves to a sudden increase in PPFD showed mean induction period (T_{100}) of 3-41 min before P_{Nmax} was reached (Table 3). The time required to reach full induction (T_{100}) depended on the background PPFDs. The higher background PPFD before an increase in PPFD, the faster the photosynthetic induction responses were. The mean time required to reach full induction was 2.5- to 3.4-fold longer when PPFD was increased from darkness than when PPFD was increased from 100 μmol m^{-2} s^{-1} except for *V. furcatum* grown in the understory. *V. furcatum* grown in the understory exhibited the shortest induction period (3.3 min) when PPFD was increased from 100 μmol m^{-2} s^{-1}, and about an 6.5-fold longer induction period when PPFD was increased from darkness compared with 100 μmol m^{-2} s^{-1}. *F. crenata* exhibited the longest induction period (T_{100}) except at background PPFD of 25 μmol m^{-2} s^{-1} in the understory. When PPFD increased from darkness, the induction period (T_{100}) was significantly shorter in understory seedlings than in gap seedlings for *V. furcatum* (Table 3, $p = 0.017$). In *F. crenata*, the mean induction period was shorter in the understory seedlings than in the gap seedlings, whereas in *A. rufinerve*, the mean induction period was shorter in the gap seedlings than in the understory seedlings. However, there were no significant differences in the induction period between the gap and the understory in *F. crenata* and *A. rufinerve* ($p > 0.05$). When PPFD increased from 25, 50, and 100 μmol m^{-2} s^{-1}, the mean induction periods (T_{100}) were shorter in the understory than in the gap for all three species. However, there was no significant difference in the induction period between the gap and the understory ($p > 0.05$). In the gap, there was no significant difference in the induction period between species ($p > 0.05$), whereas in the understory, *F. crenata* required a longer induction period than *V. furcatum* except at background PPFD of 25 μmol m^{-2} s^{-1}.

Table 3. Time [min] to reach 50, 90, and 100 % of steady-state maximum net photosynthetic rates (P_{Nmax}) during induction for leaves of the studied species. PPFD [μmol m^{-2} s^{-1}] was increased to 1 000 μmol m^{-2} s^{-1} from darkness and three different background PPFDs. Means for three leaves each from a different tree ± SD.

Plant	Background PPFD	Gap			Understory		
		T_{50}	T_{90}	T_{100}	T_{50}	T_{90}	T_{100}
Fagus crenata	0	10.7±7.4	27.5±13.8	41.0±15.9	7.5±2.9	18.3±3.6	34.3±4.4
	25	3.0±1.6	12.8±4.4	27.8±6.0	1.0±0.8	6.7±1.1	18.6±5.1
	50	2.0±0.9	12.5±4.7	23.0±4.4	-	5.2±2.7	17.3±2.5
	100	-	4.4±1.7	13.9±5.9	-	1.7±0.6	11.5±2.7
Acer rufinerve	0	7.0±3.1	16.4±7.2	26.5±7.4	10.2±3.4	18.3±6.9	28.1±12.4
	25	3.3±2.2	14.7±5.4	24.0±6.4	0.3±0.3	9.9±7.0	20.7±10.5
	50	0.4±0.3	9.4±1.9	16.6±4.3	-	2.9±0.5	9.1±1.2
	100	-	3.5±1.4	10.5±2.4	-	0.8±0.7	8.4±7.0
Viburnum furcatum	0	7.6±3.2	20.0±3.5	35.0±0.6	4.4±1.9	12.8±5.7	21.4±3.1
	25	3.6±2.9	11.1±5.3	22.3±4.7	0.1±0.1	5.3±1.9	15.8±6.6
	50	0.8±0.9	11.0±5.3	21.9±6.4	-	1.5±1.2	9.3±3.7
	100	-	3.7±1.7	12.1±4.9	-	0.1±0.0	3.3±0.3

To evaluate initial biochemical and stomatal limitations to dynamic photosynthetic performance, the relationship of relative initial photosynthetic rate to P_{Nmax} and relative initial g_s to g_{smax} *versus* induction period (T_{100} and T_{50}) are shown in Fig. 2. As initial P_N and initial g_s increased, the induction period became shorter. The induction period (T_{100}) decreased linearly with increase in the initial P_N and initial g_s (Fig. 2*A,B*), whereas the induction period (T_{50}) was negative exponentially related to the initial P_N and initial g_s (Fig. 2*D*). Plots of initial P_N and initial g_s *versus* induction period for the gap and understory showed similar patterns.

The effect of initial g_s on photosynthetic induction: The photosynthetic induction responses in leaves of *F. crenata* seedlings grown in the gap are shown in Fig. 3. PPFD was increased from darkness (0 μmol m^{-2} s^{-1}) to 1000 μmol m^{-2} s^{-1}. The time course of induction varied by a sigmoidal increase in P_N when initial g_s was low (0.01 mol m^{-2} s^{-1}). Meanwhile, P_N increased hyperbolically when initial g_s was high (0.04 mol m^{-2} s^{-1}). At both examinations, the initial P_N before the increase in PPFD was almost the same (0.2 μmol m^{-2} s^{-1}), indicating that initial biochemical limitations were similar. However, initial g_s before the increase in PPFD was different.

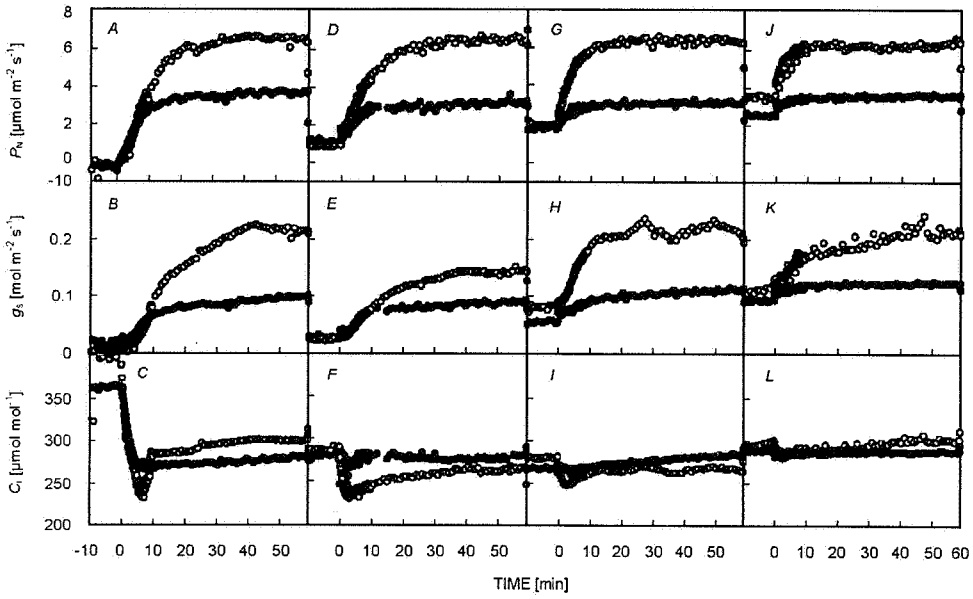

Fig. 1. Time courses of net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) during photosynthetic induction in leaves of *F. crenata* seedlings grown in the gap (*open circles*) and the understory (*closed circles*). After about 1-h at low background PPFD, PPFD was increased to 1 000 μmol m^{-2} s^{-1}. PPFD was increased from darkness (0 μmol m^{-2} s^{-1}) for the first column, from 25 μmol m^{-2} s^{-1} for the second column, from 50 μmol m^{-2} s^{-1} for the third column, and from 100 μmol m^{-2} s^{-1} for the fourth column, respectively.

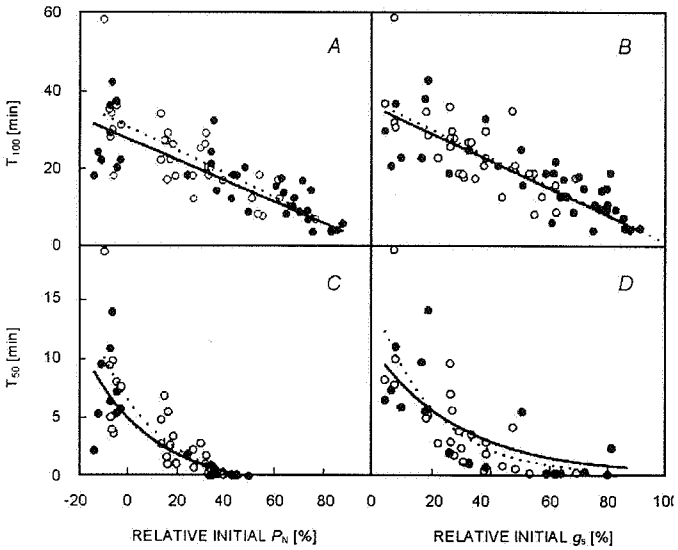

Fig. 2. Relationship between induction period (T_{100}, T_{50}) and initial net photosynthetic rate (P_N) to maximum P_N (P_{Nmax}) (*A, C*), and initial stomatal conductance (g_s) to maximum value (g_{smax}) (*B, D*), respectively. Times to 100 and 50 % induction (T_{100} and T_{50}) indicate the length of time taken to achieve 100 and 50 % of P_{Nmax}. Initial P_N and initial g_s were obtained at background PPFD before increase in PPFD. *Open circles* and *dotted lines* are for leaves grown in the gap. *Closed circles* and *solid lines* are for leaves grown in the understory.

To separate stomatal and biochemical limitations during photosynthetic induction, the steady-state photosynthetic response to C_i was plotted (Fig. 4). When initial g_s was 0.04 mol m^{-2} s^{-1}, P_N fell along the steady-state CO_2 photosynthetic response curve quickly and straight, indicating that photosynthetic induction was primarily limited by biochemical factors. On the other hand, when initial g_s was 0.01 mol m^{-2} s^{-1}, P_N fell along the steady-state CO_2 photosynthetic response curve gradually, indicating that photosynthetic induction was limited more by stomata than when the initial g_s was 0.04 mol m^{-2} s^{-1}.

The time required to reach full induction was shorter with high initial g_s than with low initial g_s (Table 4). The time required to reach full induction depended on initial

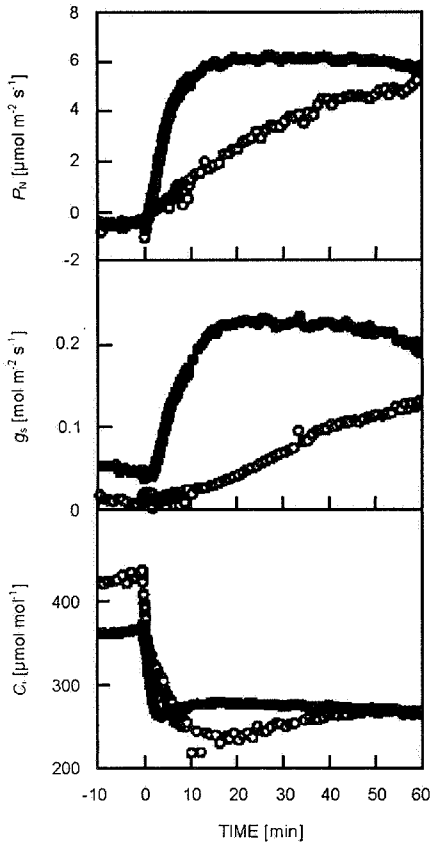

Fig. 3. The effect of initial stomatal conductance (g_s) on photosynthetic induction. Time courses of net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) during photosynthetic induction in leaves of *F. crenata* seedlings grown in the gap. PPFD was increased to 1 000 μmol m^{-2} s^{-1} from darkness (0 μmol m^{-2} s^{-1}). Initial g_s values before increase in PPFD were 0.01 (*open circles*) and 0.04 (*closed circles*) mol m^{-2} s^{-1}, respectively.

Table 4. The effect of initial stomatal conductance (g_s) [mol m^{-2} s^{-1}] on photosynthetic induction. Time [min] to reach 50, 90, and 100 % of steady-state maximum net photosynthetic rates (P_{Nmax}) during induction at gap-grown seedlings for *F. crenata*. PPFD was increased from darkness to 1 000 μmol m^{-2} s^{-1} ($n = 1$).

Initial g_s	T_{50}	T_{90}	T_{100}
0.01	19.1	43.4	58.7
0.04	4.0	11.9	22.1

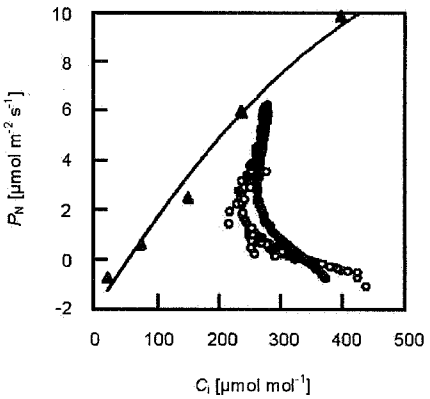

Fig. 4. Net photosynthetic rate (P_N) during photosynthetic induction plotted against intercellular CO_2 concentration (C_i) in leaves of *F. crenata* seedlings grown in the gap. PPFD increased to 1 000 μmol m^{-2} s^{-1} from darkness. Initial stomatal conductance before increase in PPFD was 0.01 (*open circles*) and 0.04 (*closed circles*) mol m^{-2} s^{-1}, respectively. Values are the same as were plotted in Fig. 3. *Closed triangles* and *line* are the steady-state relationship between P_N and C_i measured at PPFD of 700 μmol m^{-2} s^{-1} for the same leaf.

Discussion

In both plant species, P_{Nmax} was significantly higher in gap seedlings than in understory seedlings. These results were consistent with many studies (Chazdon 1986, Kitajima 1994, Liang *et al.* 1995, Chen and Klinka 1997, Murchie and Horton 1997, Han *et al.* 1999). Some studies (Lichtenthaler *et al.* 1981, Han *et al.* 1999) reported that P_N was higher at low PPFD in the understory than in the gap. We did not observe this trend except for P_{N25} in *V. furcatum*. However, relative P_N to P_{Nmax} was significantly higher in understory seedlings than in gap seedlings ($p < 0.1$). These results suggested that leaves of the understory seedlings used low PPFD more efficiently than the gap seedlings, not quantitatively, but relatively. In the gap, *A. rufinerve* exhibited more than 1.2-fold higher P_{Nmax} values than *F. crenata* and *V. furcatum*. In the understory, *F. crenata* exhibited the highest P_{Nmax} values of the three species.

g_s. When initial g_s before increase in PPFD was high, the photosynthetic induction response was fast.

There was no significant difference in induction period (T_{100}) from darkness (0 μmol m^{-2} s^{-1}) between the gap and the understory except for *V. furcatum* (Table 3). The mean induction periods (T_{100}) were shorter in the understory-grown seedlings than in the gap-grown seedlings for *F. crenata* and *V. furcatum*, and longer in the gap-grown seedlings than in the understory-grown seedlings for *A. rufinerve*. Some studies showed that the induction period was shorter in understory-grown seedlings than in gap-grown seedlings (Pons and Pearcy 1992, Küppers and Schneider 1993, Tang *et al.* 1994, Chen and Klinka 1997). Kursar and Coley (1993) described that the induction times for leaves from the gap and understory plants were indistinguishable. Poorter and Oberbauer (1993) observed that a climax species of saplings grown in shady sites had faster rates of induction than saplings grown in bright sites, in contrast there was no difference

in induction period for saplings of pioneer species. In this study, as the background PPFD before increase in PPFD increased, photosynthesis induction responses were fast (Table 3). This result was consistent with previous studies (Sassenrath-Cole and Pearcy 1994). They indicated that the biochemical induction varied as a function of the magnitude of PPFD before increase in PPFD. As the background PPFD increased, not only the initial P_N but also the initial g_s before increase in PPFD increased, indicating that the degrees of biochemical and stomatal limitations to dynamic photosynthetic performance decreased. Therefore, as the initial P_N and initial g_s increased, the time required to reach induction was shorter (Fig. 2). Photosynthetic induction response to a sudden increase in PPFD can be separated into two phases: a fast-induction phase which requires 1-2 min for the regeneration of RuBP and the build up of Calvin-cycle metabolites (Kischbaum and Pearcy 1988, Sassenrath-Cole and Pearcy 1992), followed by a slow-induction phase, lasting 5-30 min or more, in which RuBPCO is activated and stomata open (Kischbaum and Pearcy 1988, Pearcy 1990). Some studies show that stomata play a major role (Chazdon 1988, Valladares *et al.* 1997, Han *et al.* 1999), whereas other studies show that biochemical capacity is a major limitation during the slow phase of induction (Pons *et al.* 1992, Kursar and Coley 1993). Approximately the first 10 min in the slow-induction phase are dominated by PPFD activation of RuBPCO (Pons *et al.* 1992). The induction period T_{100} decreased linearly with increase in the initial P_N and initial g_s (Fig. 2*A,B*), whereas the induction period T_{50} was negative exponentially related to the initial P_N and initial g_s (Fig. 2*C,D*). The mean times required for reaching 50 % of P_{Nmax} (T_{50}) were within 11 min (Table 3). These results suggest that the limitation by the activation of RuBPCO decrease dramatically at the beginning of the slow-induction phase at background PPFD 25 and 50 μmol m^{-2} s^{-1} compared with darkness.

The relationships of these initial limitations to photosynthetic induction *versus* the induction period were similar between the gap and the understory. Initial P_N values before increase in PPFD were 72.8-81.9 % of P_{Nmax}, and the initial g_s was 71.0-84.9 % of g_{smax} at 100 μmol m^{-2} s^{-1} for the three species grown in the understory (Table 2). On the other hand, the initial P_N was 55.6-66.3 % of P_{Nmax}, and the initial g_s was 48.4-78.8 % of g_{smax} at 100 μmol m^{-2} s^{-1} for the three species grown in the gap. Except when PPFD increased from darkness, the relative initial P_N and g_s were higher in the understory-grown seedlings than in the gap-grown seedlings. The difference in time between the gap and the understory required to reach induction might reflect the varying of the relative initial P_N and g_s at background PPFD.

When initial g_s before increase in PPFD was different with the same background PPFD, photosynthetic induction responses depended on initial g_s. The time required to reach full induction was about 2.5-fold longer with low initial g_s (0.01 mol m^{-2} s^{-1}) than with high initial g_s (0.04 mol m^{-2} s^{-1}) in the gap-grown seedlings for *F. crenata* (Table 3). When initial g_s was high, photosynthetic induction was primarily limited by biochemical factors. On the other hand, when initial g_s was low, photosynthetic induction was limited mainly by stomata (Fig. 4). This result is consistent with other studies (Tinoco-Ojanguren and Pearcy 1993, Valladares *et al.* 1997, Allen and Pearcy 2000). They described that the time required for induction increased dramatically when the initial g_s was below the threshold value in the case of PPFD change from darkness to saturation. In this study, different initial g_s (0.01 and 0.04 mol m^{-2} s^{-1}) were thought to be below and above the threshold value, respectively.

There was no significant difference in the induction period between species grown in the gap ($p > 0.05$), whereas in the understory *F. crenata* required a longer induction period than *V. furcatum* except when PPFD was increased from 25 μmol m^{-2} s^{-1}. However, *F. crenata* exhibited the longest mean induction period (T_{100}) except at background PPFD of 25 μmol m^{-2} s^{-1} in the understory (Table 3), and the lowest relative initial P_N and g_s except for initial g_s at background PPFD of 100 μmol m^{-2} s^{-1} in the understory (Table 2). The difference in time required to reach induction between species as well as between the gap and the understory was also thought to mainly reflect the varying of relative initial induction states in P_N and g_s at background PPFD.

Under natural environments, the relative frequency of PPFD below 100 μmol m^{-2} s^{-1} was over 60 % in the gap (Table 1), whereas in the understory the relative frequency of PPFD below 50 μmol m^{-2} s^{-1} was over 70 %. The irradiances contributing during most of the day were considered to be diffuse irradiation in the gap and the understory. This diffuse irradiation was considered as background PPFD in this study. When the background PPFD was 100 μmol m^{-2} s^{-1}, the mean induction period (T_{100}) ranged from 9.6 to 13.9 min in the gap-grown seedlings (Table 3). When the background PPFD was 50 μmol m^{-2} s^{-1}, the mean induction period (T_{100}) ranged from 9.1 to 17.3 min in the understory-grown seedlings. The times required for reaching full induction to increase in PPFD were similar, indicating that photosynthetic responses to a sudden increase in PPFD (such as sunflecks between the gap and the understory) were almost the same under natural irradiances.

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