

論文 (Original article)

Balance of leaf traits is important for whole-plant carbon balance in shade: a study for understory saplings in a subtropical forest in Japan

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Abstract

In the understory of an evergreen forest, how leaf traits and light availability affect whole-plant carbon balance is less investigated. We predicted that variety of leaf traits can contribute to maintain whole-plant carbon balance positive in a shaded understory, and tested it in a subtropical forest in Japan, where typhoon disturbance is relatively frequently occurred. We estimated the potential net assimilation rate (NAR) of understory sites, including typhoon-disturbed sites, by measuring photosynthetic active photon flux density (PPFD). Then, for understory saplings we applied our original 'leaf relative growth rate' (RGR_{leaf}) method to simulate the whole-plant carbon balance according to its relation to leaf mass per area (LMA), leaf lifespan (LL), net assimilation rate (NAR), and leaf partitioning rate (LP). $RGR_{leaf} > 0$ indicates positive growth. Under the fully closed canopy the potential NAR was estimated to be $< 50 \text{ g glucose m}^{-2} \text{ yr}^{-1}$, where most species were predicted to have a negative RGR_{leaf} . However, with a better NAR of the site which had likely experienced a past typhoon attack, most species would have positive RGR_{leaf} . With those low-level NAR, neither LMA nor LL had significant relationships to RGR_{leaf} . There, saplings' LMA and LL showed positive relationship, but LMA tended to be smaller relative to LL compared to known global trend. With higher-level NAR, it is predicted that having smaller LMA and LL is advantageous to have large RGR_{leaf} . We concluded that balance of the leaf traits is important to maintain positive whole plant carbon balance in the low light understory, and then, various leaf traits were valid for growth in a low light understory. The moderate shade environment brought by typhoon disturbances may help to exist species with various leaf traits.

Key words : forest regeneration, leaf life span, leaf mass per area (LMA), light environment, photosynthesis, relative growth rate (RGR), shade tolerance

Introduction

The feature and performance of shade-tolerant tree species has long been discussed, mainly in comparison with light-demanding species (e.g., Givnish 1988, King 1994, Kitajima 1994, Reich et al. 1998, Kobe 1999, Walter and Reich 1999, Lusk 2002, Baltzer and Thomas 2007, Lusk and Jorgensen 2013). On the other hand, variety among saplings in a low-light forest understory have been less investigated. Regarding the characteristics of shade-tolerant species, previous studies found that lowering the light compensation point of whole-plant growth is one of the most effective strategies (Baltzer and Thomas 2007, Lusk and Jorgensen 2013). Then, potential of positive growth under a low light availability and its relationship to plant traits are worth investigating to understand species variety in a forest floor.

To evaluate whole plant growth potential and its relationship to leaf functional traits, growth analysis theory (Evans 1982) is thought to be profitable, in particular, relative growth rate (RGR) (abbreviations are listed on Table 1), which is biomass gain per plant mass per time, has long been applied. In many

Table 1. Abbreviations

A_{max}	Maximum leaf assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
A_{net}	Instantaneous leaf assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
LMA	Leaf mass per area (g m^{-2})
LL	Leaf lifespan (years)
LMR	Leaf mass ratio, the ratio of leaf mass to whole plant mass (g g^{-1})
LP	Leaf partitioning rate, the ratio of leaf mass gain to whole plant mass gain (g g^{-1})
NAR	Net assimilation rate ($\text{g glucose m}^{-2} \text{ time}^{-1}$)
PPFD	Photosynthetically active photon flux density ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
R_d	Dark respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
RGR_{leaf}	Leaf relative growth rate ($\text{g g}^{-1} \text{ year}^{-1}$)
RMR	Root mass ratio, the ratio of root mass to whole plant mass
SMR	Stem mass ratio, the ratio of stem mass to whole plant mass

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cases, RGR is composed by net assimilation rate (NAR), leaf mass per area (LMA), and leaf mass ratio to whole plant mass (LMR). However, although shade-tolerant species often have tissues of low turnover rates, and leaf lifespan (LL) should be a key trait for their carbon balance (Kikuzawa 1991, King 1994, Lusk 2002, 2004), RGR does not include LL. Then, RGR cannot be said suitable for growth potential of shade-tolerant species. Based on this, we proposed using our indicator of the whole-plant carbon balance, the leaf relative growth rate (RGR_{leaf} ; Miyashita and Tateno 2014). RGR_{leaf} has very similar basic structure to the standard RGR, but is focusing only on leaf biomass budget. This contains LL and leaf partitioning rate (LP, proportion of leaf mass gain to whole plant mass gain) as isolated parameters instead of LMR (see ' RGR_{leaf} ' in *Materials and Methods*). Using RGR_{leaf} , we can test effect of LL to whole-plant carbon balance quantitatively, then can precisely predict plant growth potential in a very low-productivity. Actually, our previous study found that (standard) RGR can overestimate seedling growth potential in the very low-light environment (Miyashita and Tateno 2014). Further, use of RGR_{leaf} allows the relationships between leaf traits and possibility of positive growth to be easily understood, and it provides the benefit of evaluating the LL.

Understory 'shade-tolerants' has been suggested to have variety of leaf traits. Montgomery and Chazdon (2001, 2002) reported that even beneath the overstory with no visible gaps, there is spatial gradient of light availability, and that growth responses of species to light availability show different patterns. These findings indicate that not only one kind of 'shade-tolerance', for example, those allows to endure and survive long period of deep shade, is valid for the understory growth. Then, variety of leaf traits should be tested with understory light availabilities. The light availability for a sapling can be represented by NAR in the RGRs. NAR can be estimated using a light-response curve of the CO_2 assimilation rate with incident photosynthetically active photon flux density (PPFD) on the leaf surface. However, understory NAR estimation based on detailed PPFD data is limited, although under field conditions, long-term light availability is unpredictable due to influences of weather conditions and other incidental elements (Miyashita et al. 2012).

In this study we simulated whole plant growth potential, or, RGR_{leaf} , of saplings with various leaf traits in the understory of subtropical forest in Japan. First, to estimate NAR, we made detailed PPFD measurement at several understory sites. We also conducted measurement of growth and the leaf traits of saplings found at apparently the lowest light availability. Then, we compared RGR_{leaf} of saplings with the potential NAR at each site. During the experimental period, about 4 months after the beginning of PPFD measurement, two severe typhoons

struck the region. Thus, we were able to monitor differences in PPFD (and consequently NAR) and LMA of the saplings before and after the disturbances, and also reported it. Finally, we discuss leaf traits diversity and importance of canopy disturbance at the forest floor from the perspective of whole-plant carbon balance.

Materials and methods

Site descriptions

This study was conducted in the Yona Experimental Forest (26°44'N, 128°14'E, 300 m above sea level) on Okinawa Island, southern Japan. The forest is located in a subtropical zone, and the surrounding natural forest is dominated by evergreen broad-leaved trees (*Castanopsis sieboldii*, *Distylium racemosum*, *Schima wallichii*, and *Elaeocarpus japonicus*; Enoki 2003, Kubota et al. 2005). The canopy surface is relatively homogeneous and lacks emergent trees. The canopy height is 7–10 m, the maximum height is < 20 m, and the canopy along ridges has a height of 5–6 m and an indistinct layer structure that is considered an effect of strong winds (Shinzato et al. 1986, Enoki 2003).

Our study took place from May 2012 to May 2014. During this period, the mean air temperatures were 26.3°C in the warmest month (July) and 13.2°C in the coldest month (January). The mean annual precipitation was 2652 mm. During the experimental period, 18 typhoons were recorded on the island (Japan Meteorological Agency). Among these, two remarkably severe typhoons struck, on 27 August 2012 and 29 September 2012. These typhoons uprooted or broke some trees in the experimental forest, and slope failures occurred in several places around the region. Right beneath a large gap, many fallen branches and stems were folded. However, around our experimental sites (mentioned below), no remarkable damage was observed for ground surface or saplings in the understory.

We chose five sites to cover various light availabilities of forest floor in the Yona Experimental Forest: at four understory locations where the canopy had been disturbed by typhoons in 2012 (gap-gap sites 1 and 2, and closed-gap sites 1 and 2, in the name, first and second "gap" or "closed" words represent the overstory condition of the sites before and after disturbance, respectively), and a site that faced a forest road and had no overstory was also selected (open site). The four disturbed sites were along a gently sloping ridge. Among these locations, the gap-gap sites were originally better lit than the closed-gap sites, and before the disturbances in 2012, these overstories were partly open, relatively low, and uneven, and saplings < 1 m occurred intermittently in the respective understories. The closed-gap sites originally had relatively high, closed, and even overstories and sparse understory vegetation. These

sites showed similar understory species composition. After the disturbance, these four sites had several small gaps and nearby large gaps $\geq 5 \text{ m}^2$.

Collection of environmental data

Correlation chart of measured data and estimated values is shown in Fig. 1.

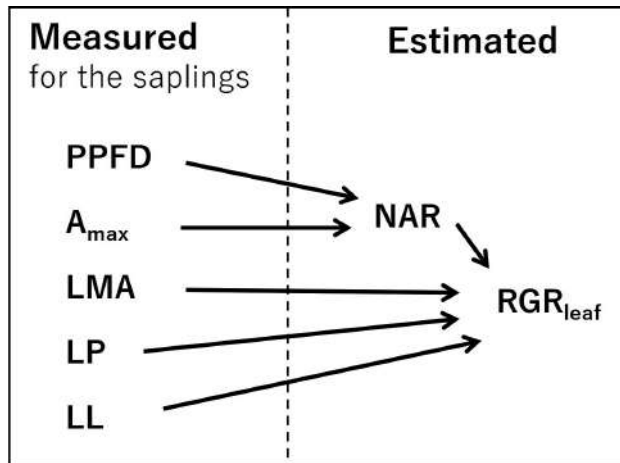


Fig. 1. Correlation chart of measured and estimated values.

PPFD and air temperature were measured at all five sites. At each site we placed one quantum sensor (Photosynthetic Light (PAR) Smart Sensor - S-LIA-M003; Onset Computer, Pocasset, MA, USA) and one temperature sensor (12-bit Temperature Smart Sensors; Onset Computer Corp.). The quantum sensors were set 30 cm above the ground and

carefully leveled. Understory saplings that might have covered the sensors were removed. A datalogger (HOBO Micro Station Data Logger; Onset Computer) was connected to the quantum and temperature sensors to sample the sensor output [PPFD ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) and air temperature ($^{\circ}\text{C}$)] every minute, an interval that was considered sufficiently short to capture short-term fluctuations such as sunflecks while keeping the quantity of data manageable (cf. Pearcy 1983). Measurements were conducted from 10 May 2012 to 26 May 2014. At the open site, the data logger stopped recording due to an unknown cause during the period 30 October 2012 to 16 January 2013, so data were not collected at this site during this period.

Determination of sapling leaf traits

For naturally occurring saplings at closed-gap site 2 that were within a $\sim 5\text{-m}$ radius of the quantum sensor, we made the following measurements. Because there was scarce vegetation at the site, we sampled from all saplings included evergreen broad-leaved trees or shrubs $\leq 1 \text{ m}$ in height, except for individuals visibly damaged. Number of sampled individuals was one, and two only for *Dendropanax trifidus*. For details of the saplings, species, size and leaf traits, see Table 2 and 3.

LMA was determined twice for the same individual, in May 2012 (before the disturbance) and in May 2014 (after the disturbance). We collected five or more sample leaves from each sapling including leaves of various ages. The leaves were scanned to determine leaf area and then oven-dried at 80°C for 48 hours to determine dry mass.

Table 2. Study individuals found at closed-gap site 2.

Species	Adult Stature	Height (cm)	Whole Plant Mass (g)	Leaf Mass Ratio (g g^{-1})	Stem Mass Ratio (g g^{-1})	Root Mass Ratio (g g^{-1})
<i>Bredia okinawensis</i>	shrub	46	19.3	0.34	0.48	0.18
<i>Castanopsis sieboldii</i>	canopy tree	21	10.1	0.49	0.32	0.20
<i>Cinnamomum doederleinii</i>	canopy tree	50	20.4	0.46	0.38	0.16
<i>Cinnamomum yabunikkei</i>	sub-canopy tree	80	8.6	0.44	0.36	0.20
<i>Dendropanax trifidus</i>	canopy tree	25	2.9	0.41	0.34	0.24
<i>Dendropanax trifidus</i>	canopy tree	64	24.3	0.21	0.63	0.16
<i>Distylium racemosum</i>	canopy tree	75	29.9	0.19	0.60	0.21
<i>Hydrangea liukiensis</i>	shrub	60	14.5	0.16	0.48	0.36
<i>Lasianthus fordii</i>	shrub	72	17.1	0.23	0.52	0.25
<i>Machilus thunbergii</i>	canopy tree	53	8.3	0.30	0.40	0.30
<i>Myrsine seguinii</i>	canopy tree	75	17.4	0.24	0.53	0.23
<i>Neolitsea aciculata</i>	sub-canopy tree	47	7.6	0.38	0.29	0.33
<i>Skimmia japonica</i>	shrub	73	59.3	0.20	0.25	0.56
<i>Syzygium buxifolium</i>	canopy tree	108	85.9	0.17	0.49	0.34

LL was estimated in the following ways, when it was difficult to determine LL precisely during the experimental period. First, we determined the age of the oldest leaf cohort by observing the shoot elongation pattern (most species had a clear seasonal pattern of shoot growth). We assumed this age to be the maximum LL (LL_{\max} , year). This observation was conducted in May 2012. Second, we observed the 1-year leaf turnover rate, following Lusk (2014), and then used its inverse as LL_{obs} , i.e., $LL_{\text{obs}} = (\text{number of leaves present at outset}) / (\text{number of leaves shed during 1 year})$. For this observation, we photographed the same branches in May 2013, September 2013, January 2014, and May 2014 and observed changes in leaf numbers and shoot elongation patterns. Because most species in this area apparently have an LL of around 1–2 years, we did not distinguish LL before the disturbances from that after the disturbances in the observation of the leaf cohort in May 2013. Between LL_{\max} and LL_{obs} , we used the smaller one for sapling LL in order to exclude extremely long LL, which can be estimated because of limitation of observation period and number of samples. The LL determination was conducted for three to four branches per sapling, or for one main stem. The average values of branches or stems were used to determine the species LL at each site.

LP was estimated by one-year above ground growth tracking (May 2013– May 2014) and final whole-plant harvest in May 2014. Because direct determination of LP requires repeated destructive sampling, we could only estimate. We estimated

the maximum and minimum values of LP to present a potential range of RGR_{leaf} for each individual. LP_{\max} is determined only by above ground mass change regardless of root mass, i.e., $LP_{\max} = \text{leaf mass gain} / \text{above ground mass gain}$, expecting the maximum value of LP. LP_{\min} is calculated using root mass ratio (RMR) as, $LP_{\min} = LP_{\max} * (1 - \text{RMR})$, assuming that the mass fractions are directly reflected to tissue investment rates, although LP tend to be larger than LMR (Veneklaas and Poorter 1998, Miyashita and Tatenno 2014). Above ground mass gain was determined by the one-year change in stem volume and leaf area. After final harvest, we determined stem density and LMA, then, using it, they were altered to mass growth. We assumed that a sapling architecture consisted of main stem(s) and some iteration of components of branches and leaves. Then, for main stem(s), and for all branches and leaves of one component, we tracked one-year growth, and multiplied it to estimate whole above ground growth. For stem volume diameters at two direction were measured at least three points (base, middle, tip) per stem or branch. We determined stem density using the calculated volume and dry weight for three stems or branches per individual, then, averaged them. For leaf area, we measured leaf number change and average leaf size together with LL estimation.

Photosynthetic capacity of the understory saplings was also determined. The maximum photosynthetic rate (A_{\max}) and dark respiration rate (R_d) of leaves were measured on May 29 and 30, 2013, (after the disturbance) for 19 individuals from 15

Table 3. The leaf traits of study saplings at closed-gap site 2.

Species	May, 2012		May, 2014		LL (yr)
	LMA	LMA	LP(max)*	LP(min)**	
	(g m ⁻²)	(g m ⁻²)	(g g ⁻¹)	(g g ⁻¹)	
<i>Bredia okinawensis</i>	53	65	0.56	0.46	1.9
<i>Castanopsis sieboldii</i>	79	104	0.59	0.47	2.5
<i>Cinnamomum doederleinii</i>	99	122	0.52	0.44	3.3
<i>Cinnamomum yabunikkei</i>	40	104	0.43	0.34	2.0
<i>Dendropanax trifidus</i>	59	50	0.64	0.48	1.8
<i>Dendropanax trifidus</i>	40	66	0.54	0.45	1.8
<i>Distylium racemosum</i>	115	136	0.74	0.58	2.6
<i>Hydrangea liukiuensis</i>	17	33	0.66	0.42	0.7
<i>Lasianthus fordii</i>	43	63	0.47	0.35	1.6
<i>Machilus thunbergii</i>	84	109	1.00a	0.84	2.5
<i>Myrsine seguinii</i>	79	118	0.59	0.46	2.0
<i>Neolitsea aciculata</i>	62	72	0.57	0.38	2.0
<i>Skimmia japonica</i>	62	107	1.00 a	0.50	2.0
<i>Syzygium buxifolium</i>	65	97	0.26	0.17	3.0

*: LP values derived only from the above ground (leaf and stems) mass gain, $LP_{\max} = (\text{leaf mass gain}) / (\text{above ground mass gain})$.

** : LP values considering the root mass ratio (RMR), $LP_{\min} = LP_{\max} * (1 - \text{RMR})$. *: In the case of stem mass gain ≤ 0 , LP_{\max} is assumed as 1.0.

species around closed-gap site 2 (one leaf per individual, and one to three individuals per species, including individuals not listed on Tables 2 and 3). A branch was collected from each sapling before dawn, brought back to the laboratory in a plastic bag (within 30 min), and then immediately severed again under water. We then selected one fully expanded, young-to medium-aged leaf from each branch. The measurements were made in the early to late morning using an infrared gas-exchange analyzer (Li-6400; Li-Cor, Lincoln, NE, USA) with an ambient CO₂ concentration of 400 µmol mol⁻¹, leaf temperature of 25°C, and relative humidity of 75% and, for A_{max} measurements, a saturated PPFD of 1,500 µmol m⁻² s⁻¹.

Estimating the potential NAR of understory sites

The net assimilation rate (NAR: g glucose m⁻² year⁻¹) at each site was calculated by summing up the instantaneous net assimilation rates of leaves (A_{net}, µmol CO₂ m⁻² s⁻¹) and converting them to the mass of glucose (180 g mol⁻¹) to be comparable with biomass. We calculated one-year unit NAR for the use of RGR_{leaf} using three periods of PPFD: First, NAR for 'before the disturbances', we used PPFD during May–August 2012. Second, for NAR 'soon after' the disturbances, we used PPFD during Sep 2012–August 2013. Third, for NAR 'after the disturbances', we used PPFD during May 2013 to Apr 2014. Among those, the first period was short for one year because of the timing of typhoon attacks. We compensated this by calculating average daily NAR during the period × 365 days.

For NAR calculation, we used light-response curves for CO₂ assimilation described by a non-rectangular hyperbola (Thornley, 1976). A_{net} at a given PPFD is

$$A_{net} = \frac{\Phi * PPFD + A_{max} - \sqrt{(\Phi * PPFD + A_{max})^2 - 4\Phi * PPFD * \Theta * A_{max}}}{2\Theta} - R_d, \quad (1)$$

where A_{max} is the light-saturated rate of gross CO₂ assimilation, Φ represents the initial slope of the line (mol CO₂ mol quanta⁻¹), Θ is the curvature factor (nondimensional), and R_d is the dark respiration rate of leaves (µmol CO₂ m⁻² s⁻¹). We substituted our PPFD data into (1) and summed A_{net} assuming that PPFD lasted for 1 min. For other parameters, because we did not have the specific data, so we computed the NAR by changing the parameters separately in the range of which can cover all the possible values of understory leaves. A_{max} was changed stepwise from 1 to 20 µmol CO₂ m⁻² s⁻¹; R_d was determined relative to A_{max}; and R_d/A_{max} was set at 1/15, 1/10, and 1/7 at a leaf temperature of 25°C. Φ and Θ were set at 0.04, 0.05, and 0.07 mol CO₂ mol quanta⁻¹ and 0.5, 0.8, and 0.99, respectively. These parameters were set also referring to published works on understory or shaded evergreen broad-leaved trees (Koyama 1981, Turnbull 1991, Kitajima 1994,

Valladares et al. 1997, Thomas and Bazzaz 1998, Veneklaas and Poorter 1998, Walters and Reich 1999, Marengo et al. 2001, Feng et al. 2004, Miyazawa and Kikuzawa 2005). Temperature and PPFD dependence was also applied to R_d value following Oguchi et al. (2008): R_d was changed depending on leaf temperature relative to the value at 25°C using the Arrhenius model, and R_d was not modified when PPFD = 0 µmol m⁻² s⁻¹, but it was multiplied by 0.4 when PPFD > 0. We did not include the leaf temperature dependence of A_{max} in our calculations because air temperature during the daytime in the experimental forest was relatively even and photosynthetically favorable throughout the year. During the experimental period, > 78% of measured air temperatures (when PPFD > 0) were within the 10–25°C range.

After summing A_{net}, which is the leaf-level NAR, considering only leaf respiration rates. To convert it to the (whole-plant) NAR, we need to consider whole-plant carbon consumption (construction and maintenance respirations). We used the following expression in the calculations: NAR = (leaf-level NAR) × 0.45. It has been estimated that ~50% of assimilated glucose remains available for tissue construction and maintenance after respiratory consumption is considered (Mooney 1972), although available data of tree seedlings or saplings at the whole-plant level are scarce. We also estimated the proportion of remaining assimilated glucose during a year for seedlings of cool-temperate deciduous tree species (*Acer* and *Fagus*) growing at several small gap sites, as 32–48% (average 39%) (A Miyashita, FFPRI, unpub. data).

Statistical analyses among the leaf traits (linear regression: LL vs LMA and the leaf traits and RGR_{leaf}, *t*-test; paired two sample for means: LL in 2012 and 2014) were conducted by Excel 2013 (Microsoft Corp. Redmond, WA, USA).

RGR_{leaf}

Our indicator of whole plant growth potential, RGR_{leaf}, is calculated as follows (Miyashita and Tateno 2014),

$$RGR_{leaf} = (NAR \times LP)/LMA - (1/LL), \quad (2)$$

In the eq. (2), the part '(NAR×LP)/LMA' represents growth rate of foliage, and '1/LL' represents the mortality rate of foliage. Thus, RGR_{leaf} specifically evaluate leaf biomass growth potential. This is based on our idea of plant growth that in a condition of low productivity and steady-state, a plant never expand its biomass unless its leaf biomass (or leaf area) expand. Note that RGR_{leaf} is only designed for judge the potential of positive growth at the time of the parameters were obtained. So, it is unsuitable for a plant under fluctuating environment. Also note that the value is not the same as whole plant growth rate such as RGR. When RGR_{leaf} > 0, the whole plant carbon balance is positive and a plant potentially continues to grow. RGR_{leaf} ≤ 0 represents that a plant have

the same leaf area or reduced leaf area in the next year. This does not necessarily mean immediate death of a plant, if such condition does not continue over years.

Results

Understory light availability and leaf photosynthetic productivity

During the experimental period before the typhoons (May–August 2012), PPFD values at closed-gap sites 1 and 2 were 1.9 and 1.3% of that at the open site, or, 0.51 and 0.36 mol quanta $\text{m}^{-2} \text{day}^{-1}$ on average, respectively, while at gap-gap sites 1 and 2, the relative PPFD to the open site were 4.5 and 7.4%, or, 1.2 and 2.0 mol quanta $\text{m}^{-2} \text{day}^{-1}$, respectively (Fig. 2). After the disturbances, light availability improved remarkably at all sites. In May 2014, the PPFD values relative to the open site (RPPFD, %) at gap-gap sites 1 and 2 and closed-gap sites 1 and 2 were 13.8, 8.4, 13.1, and 14.4%, respectively. The degree of improvement was greater for sites with relatively low light availability before the disturbances. The frequency of PPFD $< 50 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is considered to represent diffuse light level (Percy 1983, Miyashita et al. 2012), decreased at all sites, and for higher level PPFD, the frequency increased. These higher PPFD levels persisted into the subsequent season, but canopy closure was observable at the beginning of 2014. For instance, relative PPFD on May 2014 was decreased to around 75% of that on May 2013, but the light availability remained relatively high at closed-gap site 2.

There is large variation of calculated NAR depending on the photosynthetic parameter set, which include unrealistic values,

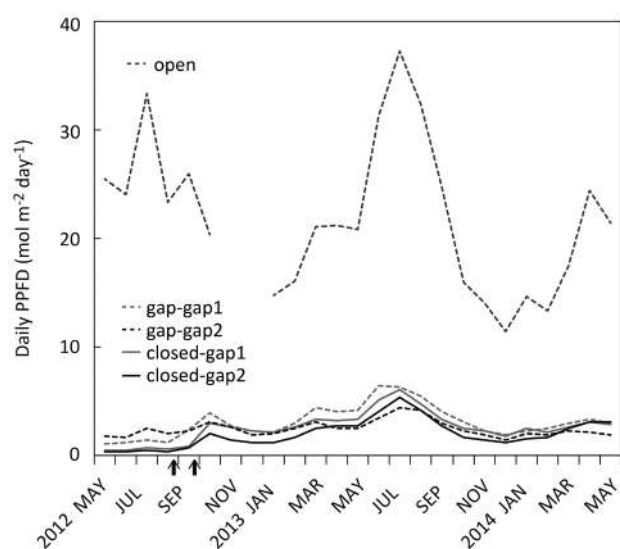


Fig. 2. Monthly trends in the mean daily total photosynthetically active photon flux density (PPFD) at each site from May 2012 to May 2014.

Arrows indicate the dates on which the typhoons struck.

though (Appendix Fig. 1). Considering that the $A_{\text{max_net}}$ values of leaves collected at closed-gap site 2 were concentrated around $4 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (Fig. 3), we chose the parameter sets giving the maximum NAR at $A_{\text{max_net}}$ around $4 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ to emphasize that understory NAR is basically too small for plant growth: The parameter set 'R10', i.e., (Φ , Θ , R_d/A_{max}) = (0.05, 0.8, 1/10) and the NAR is just about the average of all calculated NAR. Indeed, low-light understory leaves have a similar $A_{\text{max_net}}$ value regardless of species, which is almost the optimal value maximizing leaf-level NAR (Kitajima 1994, Feng et al. 2004, Miyashita et al. 2012). With regard to the maximal NAR value, NAR under fully closed and undisturbed canopies were estimated to be $< 50 \text{ g glucose m}^{-2} \text{year}^{-1}$; whereas estimates at the better lit sites exceeded $100 \text{ g glucose m}^{-2} \text{year}^{-1}$ (Table 4). NAR values of soon after the disturbances (September 2012–August 2013) were at least 1.9 times greater than those before the disturbance at gap-gap sites, and more than 7.5 times greater for closed-gap sites.

Sapling leaf traits and RGR_{leaf}

The observed LMA and LL values at closed-gap site 2 covered a wide range (Table 3). LL and LMA had a positive linear relationship [$r^2 = 0.65$ for LMA collected in 2012 (Fig. 4), and $r^2 = 0.59$ for LMA collected in 2014]. After the disturbances, the mean LMA of saplings increased significantly ($p < 0.05$). LPs had no significant relationship with LMA or LL.

With the lowest level of light availability (NAR = $50 \text{ g glucose m}^{-2} \text{year}^{-1}$), most saplings could not maintain a

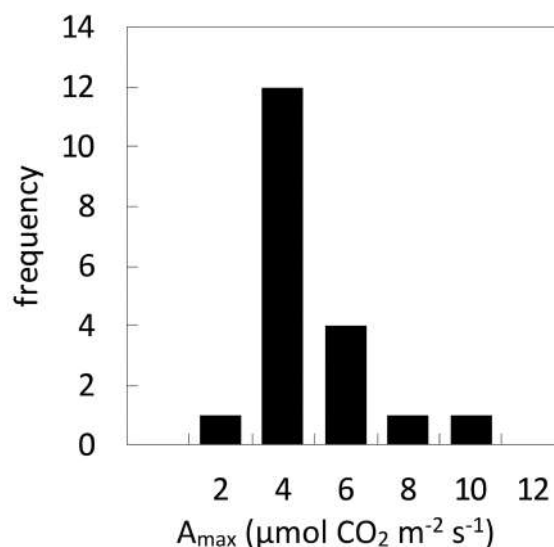


Fig. 3. Frequency distributions of leaf photosynthetic capacity ($A_{\text{max_net}}$) of saplings at closed-gap site 2 measured in May 2013.

$A_{\text{max_net}}$ is a net value (i.e., $A_{\text{max}} - R_d$; R_d , leaf dark respiration rate). For each species' value, see Appendix Table 1.

positive RGR_{leaf} (with LMA observed at May 2012, Fig. 5 a-c). When $NAR \geq 100$ g glucose m^{-2} year $^{-1}$, Many saplings have positive RGR_{leaf} (with LMA observed at May 2014, Fig. 5 d-f), which corresponds to NAR of gap-gap sites before the disturbances (Table 4). At the low level of NAR such as < 100 g glucose m^{-2} year $^{-1}$, neither LMA nor LL solely contributed to RGR_{leaf} , while LP showed weak positive correlation to RGR_{leaf} . With small values of NAR, saplings having RGR_{leaf} near and above the zero can be regarded as most shade-tolerant. Their combination of LMA and LL showed variety: for examples, *Cinnamomum doederleinii*; having relatively large LMA and LL, and *Hydrangea liukiuensis* having small LMA and LL (Table 3). At higher level of NAR such as the sites after the disturbances, both LMA and LL showed negative correlation to RGR_{leaf} : having a combination of small LMA and LL apparently be advantageous (Fig. 5 g-i).

Discussion

Leaf traits of shade tolerant species in the low-light understory

Generally, having tough and durable tissues is considered effective to attain a high survival rate, but lower the carbon gain efficiency and growth rate (Kitajima 1994, Kobe 1999). However, several studies have indicated that those enduring tissues can also contribute to carbon gain: long-lived leaves, which is concomitant with a large LMA (Reich et al. 1992 used 'SLA', which is the inverse of LMA) can contribute to maintaining a positive whole-plant carbon balance under low light availability at time scales of a year or longer (Walters and Reich 1999, Lusk 2002, 2004, Miyashita and Tatenko 2014). These studies demonstrated that evergreen shade-tolerant saplings that have leaves with relatively large LMA and long LL can accumulate canopy leaves and gain, or avoid the loss

of, carbon in a low-light environment. Therefore, it can be stated that traits associated with longevity are compatible with those that contribute to whole-plant carbon balance. On the other hand, 'fast-growth traits' also can be adoptive to low-light availability. A relatively small LMA, which is concomitant with a short LL (Reich et al. 1992), is known to clearly correlate with higher whole-plant RGR (Poorter and Remkes 1990, Walters et al. 1993, Reich et al. 1998, Walters and Reich 1999). Such sets of traits are often observed in light-demanding species (Poorter and Remkes 1990, Walters et al. 1993, Kitajima 1994, Reich et al. 1998, Walters and Reich 1999), but these traits can also be advantageous in a low-light environment because of potentially higher carbon gain efficiency. Indeed, several studies have reported a larger observed RGR for light-demanding species than for shade-tolerant species under low-light conditions (Kitajima 1994, Walters et al. 1993, Reich et al. 1998, Walters and Reich 1999, Tatenko and Taneda 2007). Therefore, our results do not contradict previous studies, and RGR_{leaf} (Equation 2) could make the theoretical integration of the effects of leaf traits on whole plant carbon balance: species with a small LMA and short LL and those with a large LMA and long LL both can be shade-tolerant depending on their balance. Therefore, shade-tolerant species in deep shade can have various combinations of leaf traits. There are also some works reported that both species having a larger LMA and LL and those having a smaller LMA and LL were found in low-light environments (King, 1994, Baltzer and Thomas 2007).

To maintain positive RGR_{leaf} in the deep shade, having a smaller LMA relative to LL is clearly effective. Considering the regression line of LMA versus LL in this study, LMA tended to be smaller than (about 70 % of) that in the reported global trend (e.g. Reich et al. 1992). It can be because of 'shade

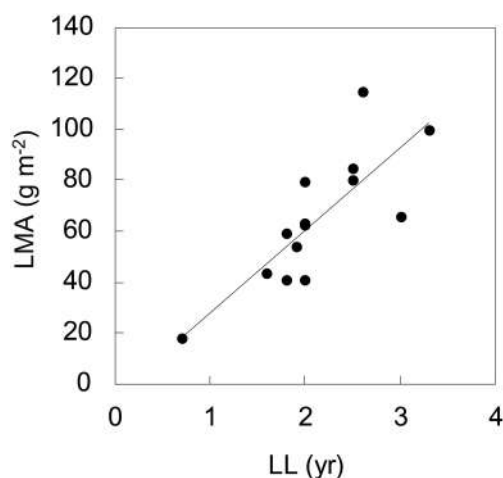


Fig. 4. Leaf mass per area (LMA, g m $^{-2}$) versus leaf life span (LL, years).

The relationship was observed for the saplings at closed-gap site 2 ($r^2 = 0.65$).

Table 4. Estimated values of NAR at each site

period	before	soon after	after
	disturbances (May 2012- Aug 2012)	disturbances (Sep 2012- Aug 2013)	disturbances (May 2013- Apr 2014)
Open	1,341	-	1,251
gap-gap1	119	442	430
gap-gap2	150	278	262
closed-gap1	43	322	338
closed-gap2	27	237	269

The NAR values calculated using PPFD data at each site and photosynthetic parameters of light response CO_2 assimilation curve which is $(A_{max}, \Phi, \Theta, R_d/A_{max}) = (4.0, 0.05, 0.8, 1/10)$, where A_{max} : the maximum photosynthetic capacity, Φ : initial slope, Θ : convexity and R_d : dark respiration rate.

leaves', which tended to have smaller LMA compared to sun leaves as presented in Onoda et al. (2011). Actually, in this study, LMA became significantly large after improvement of the light availability. For shade leaves LL-LMA relationships has been rarely investigated, but data from King (1994) shows those very similar to ours. LP also indicated to be effective for low-light growth. However, in this study LP was not directly measured, so the results need further investigation. Veneklaas and Poorter (1998), who modeled whole-plant growth of shade-tolerant trees, took 0.55 as LP on the basis of large studies evaluating plant growth allometry: In that study, the

average LMR was shown as 0.37. Our result is comparable to their study: LP values estimated for the saplings are in around 0.45-0.55, and on average, LMR was 0.30. In another study, Miyashita and Tateno (2014) reported average seedling LP values of 0.50 at a closed canopy site (cool-temperate tree species).

Understory light availability and importance of canopy disturbance

Our results suggest that no species can grow vigorously under the fully closed canopy in this forest. In the Yona

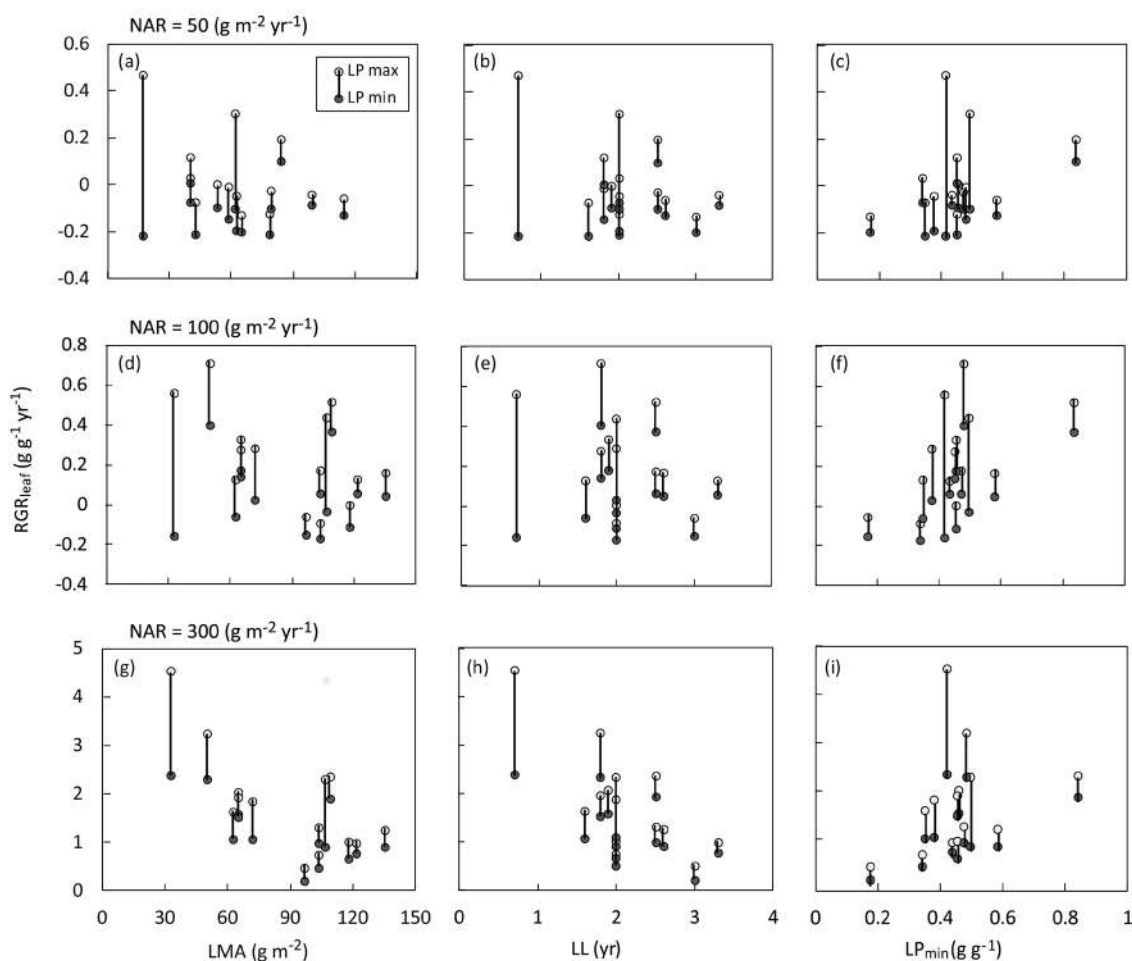


Fig. 5. Simulated RGR_{leaf} of saplings found at closed-gap site 2 shown relative to each leaf traits.

(a-c) Results calculated by using $NAR = 50 \text{ g glucose m}^{-2} \text{ yr}^{-1}$, which is corresponded to NAR beneath the fully closed overstory, and leaf mass per area (LMA) determined in 2012 before the disturbances. (d-f) Results calculated by using $NAR = 100 \text{ g glucose m}^{-2} \text{ yr}^{-1}$, which is corresponded to NAR beneath the canopy with some gaps before the disturbances (which is better lit compared to closed-gap site2 before the disturbance), and LMA determined in 2014 after the disturbances. (g-i) Results calculated by using $NAR = 300 \text{ g glucose m}^{-2} \text{ yr}^{-1}$, which is corresponded to NAR at the understory sites after the disturbances, and LMA determined in 2014 after the disturbances. (a, d, g) The result for LMA, (b, e, h) for leaf life span (LL), and (c, f, i) the minimum value of leaf partitioning rate (LP_{min}). Each line represents an individual showing the range of potential RGR_{leaf} calculated with the maximum value of LP and the minimum value of LP. For relationship of RGR_{leaf} vs each parameter, (a-c) RGR_{leaf} vs LMA, $r^2 = 0.23$ and 0.04 , RGR_{leaf} vs LL, $r^2 = 0.32$ and 0.08 , and RGR_{leaf} vs LP_{min} , $r^2 = 0.11$ and 0.47 for the case of calculation using LP_{max} and LP_{min} , respectively, (d-f) RGR_{leaf} vs LMA, $r^2 = 0.28$ and 0.01 , RGR_{leaf} vs LL, $r^2 = 0.20$ and 0.02 , and RGR_{leaf} vs LP_{min} , $r^2 = 0.28$ and 0.45 for the case of calculation using LP_{max} and LP_{min} , respectively, and (g-i) RGR_{leaf} vs LMA, $r^2 = 0.51$ and 0.46 , RGR_{leaf} vs LL, $r^2 = 0.55$ and 0.36 , and RGR_{leaf} vs LP_{min} , $r^2 = 0.10$ and 0.23 for the case of calculation using LP_{max} and LP_{min} , respectively.

Experimental Forest, the smallest class of NAR required for saplings to have a positive RGR_{leaf} was approximately $50 \text{ g glucose m}^{-2} \text{ year}^{-1}$. This value corresponded to 2% in relative PPFD and $0.5 \text{ mol m}^{-2} \text{ day}^{-1}$ in daily total PPFD. The result is comparable with those of previous studies estimating the whole-plant light compensation points of saplings: understory species were shown to require a NAR of $34\text{--}46 \text{ g m}^{-2} \text{ year}^{-1}$ (for leaf turnover, King 1994), PPFD of $0.5 \text{ mol m}^{-2} \text{ day}^{-1}$ (Lusk and Jorgensen, 2013), or $1.0 \text{ mol m}^{-2} \text{ day}^{-1}$ (Baltzer and Thomas 2007). However, there are more shade-tolerant cases, in which the light compensation points were estimated to be less than 0.5% of the relative PPFD (Poorter 1999) or approximately $0.1 \text{ mol m}^{-2} \text{ day}^{-1}$ (Lusk et al. 2015). Those high shade-tolerance may be because of so long LL (cf., Lusk et al. 2002). Also, in our previous studies of a cool-temperate deciduous–coniferous mixed forest, we found that even a shade-tolerant tree species (evergreen conifer) had difficulty maintaining a positive carbon balance under a closed evergreen (coniferous) canopy (Miyashita et al. 2012, Miyashita and Tateno 2014). These facts indicate that understory of fully closed evergreen canopy is a hard condition to grow even for a shade-tolerant tree species.

However, light availability in forest understory can be varied even under closed overstory (Montgomery and Chazdon 2001). Further, in our study site, typhoons act as a significant disturbance factor. According to the records of the Japan Meteorological Agency, the two severe typhoons that struck on 27 August 2012 and 29 September 2012 had maximum instantaneous wind velocities of 38.1 m s^{-1} and 57.4 m s^{-1} , respectively. Similar typhoons occur only once every few years and once every two decades, respectively. We thus propose that improvements in understory light availability in this forest will occur at intervals of 5 or more years. Those improvements, however, cannot continue for many years. The decrease in daily total PPFD in May 2014 (Fig. 2) suggests that even a severe disturbance does not improve light availability over few years. Before the 2012 disturbances, in the gap–gap sites that had apparently experienced a disturbance previously, the estimated NAR was around $130 \text{ g glucose m}^{-2} \text{ year}^{-1}$. This value may be sufficient for many tree species to continue to grow, but not allow for vigorous growth. Therefore, in this experimental forest, shade-tolerant species do not need to endure a very low-light availability for decades or more. Instead, they need to wait for a disturbance and continue to grow with the somewhat improved light availability.

Interestingly, such moderate-shade condition may give various species opportunity to regenerate. As suggested in Fig. 5 (g-i), at a higher light availability, species having higher efficiency of productivity (small LMA and short LL) can be further advantageous. In terms of whole plant carbon balance,

relatively low-light understory could work as a nursery for species with various leaf traits.

Conclusion

This study evaluated the saplings whole-plant carbon balance, which is considered to be an important criterion of shade tolerance. For this, we investigated photosynthetic productivity, sapling traits, and RGR_{leaf} in the understory of a subtropical evergreen forest. Then we elucidated that no single trait is advantageous for growth potential in the deep shade, instead, the balance of leaf traits is important in this subtropical forest understory. Our results indicate that most species were unable to maintain a positive whole-plant carbon balance at the fully closed overstory. However, at just a little higher-light availability, saplings having variety of the leaf traits can maintain positive growth. In future, more relationships of leaf traits which directly associate with whole-plant carbon budget, such as LMA, LL and LP, including ontogenic change and environmental plasticity, should be investigated to understand a possibility of maintaining species variety.

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References

- Baltzer, J. L. and Thomas, S.C. (2007) Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *J. Ecol.*, 95, 1208–1221. <https://doi.org/10.1111/j.1365-2745.2007.01286.x>
- Enoki, T. (2003) Microtopography and distribution of canopy trees in a subtropical evergreen broad-leaved forest in the northern part of Okinawa Island, Japan. *Ecol. Res.*, 18(2), 103–113. <https://doi.org/10.1046/j.1440-1703.2003.00549.x>
- Evans, G. C. (1972) *The Quantitative Analysis of Plant Growth*. Blackwell Scientific Publications, Oxford.
- Feng, Y. L., Cao, K. F. and Zhang, J. L. (2004) Photosynthetic characteristics, dark respiration, and leaf mass per unit area in seedlings of four tropical tree species grown under three irradiances. *Photosynthetica*, 42, 431–437. <https://doi.org/10.1007/s11099-007-0040-2>
- Givnish, T. J. (1988) Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiol.*, 15, 63–92.
- Ichihara, Y. and Yamaji, K. (2009) Effect of light conditions on the resistance of current-year *Fagus crenata* seedlings

- against fungal pathogens causing damping-off in a natural beech forest: fungus isolation and histological and chemical resistance. *J. Chem. Ecol.*, 35, 1077–1085.
- Imaji, A. and Seiwa, K. (2010) Carbon allocation to defense, storage, and growth in seedlings of two temperate broad-leaved tree species. *Oecologia*, 162, 273–281.
- Kikuzawa, K. (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern, *Am. Nat.*, 138, 1250–1263. <https://doi.org/10.1086/285281>
- King, D. A. (1994) Influence of light level on the growth and morphology of saplings in a Panamanian forest. *Am. J. Bot.*, 81, 948–957. <https://doi.org/10.2307/2445287>
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98, 419–428. <https://doi.org/10.1007/BF00324232>
- Kobe, R. K. (1999) Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, 80, 187–201. [https://doi.org/10.1890/0012-9658\(1999\)080\[0187:LGPATT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0187:LGPATT]2.0.CO;2)
- Koyama, H. (1981) Photosynthetic rates in lowland rain forest trees of Peninsular Malaysia. *Jap. J. Ecol.*, 31, 361–369.
- Kubota, Y., Katsuda, K. and Kikuzawa, K. (2005) Secondary succession and effects of clear-logging on diversity in the subtropical forests on Okinawa Island, southern Japan. *Biodiver. Conserv.*, 14, 879–901. <https://doi.org/10.1007/s10531-004-0657-4>
- Lusk, C. H. (2002) Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. *Oecologia*, 132, 188–196. <https://doi.org/10.1007/s00442-002-0974-9>
- Lusk, C. H. (2004) Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. *Funct. Ecol.*, 18, 820–828. <https://doi.org/10.1111/j.0269-8463.2004.00897.x>
- Lusk, C. H. and Jorgensen, M. A. (2013) The whole-plant compensation point as a measure of juvenile tree light requirements. *Funct. Ecol.*, 27, 1286–1294. <https://doi.org/10.1111/1365-2435.12129>
- Lusk, C. H., Jorgensen, M. A. and Bellingham, P. J. (2015) A conifer–angiosperm divergence in the growth vs. shade tolerance trade-off underlies the dynamics of a New Zealand warm-temperate rain forest. *J. Ecol.*, 103, 479–488. <https://doi.org/10.1111/1365-2745.12368>
- Marenco, R. A., Gonçalves, J. F. D. C. and Vieira, G. (2001) Leaf gas exchange and carbohydrates in tropical trees differing in successional status in two light environments in central Amazonia. *Tree Physiol.*, 21, 1311–1318. <https://doi.org/10.1093/treephys/21.18.1311>
- Miyashita, A., Sugiura, D., Sawakami, K., Ichihashi, R., Tani, T. and Tateno, M. (2012) Long-term, short-interval measurements of the frequency distributions of the photosynthetically active photon flux density and net assimilation rates of leaves in a cool-temperate forest. *Agric. For. Meteorol.*, 152, 1–10. <https://doi.org/10.1016/j.agrformet.2011.08.001>
- Miyashita, A. and Tateno, M. (2014) A novel index of leaf RGR predicts tree shade tolerance. *Funct. Ecol.*, 28, 1321–1329. <https://doi.org/10.1111/1365-2435.12290>
- Miyazawa, Y. and Kikuzawa, K. (2005) Winter photosynthesis by saplings of evergreen broad-leaved trees in a deciduous temperate forest. *New Phytologist*, 165, 857–866. <https://doi.org/10.1111/j.1469-8137.2004.01265.x>
- Mooney, H. A. (1972) The carbon balance of plants. *Ann. Rev. Ecol. System.*, 3, 315–346. <https://doi.org/10.1146/annurev.es.03.110172.001531>
- Oguchi, R., Hikosaka, K., Hiura, T. and Hirose, T. (2008) Costs and benefits of photosynthetic light acclimation by tree seedlings in response to gap formation. *Oecologia*, 155, 665–675. <https://doi.org/10.1007/s00442-007-0951-4>
- Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., Díaz, S., Dominy, N.J., Elgart, A., Enrico, L., Fine, P.V.A., Howard, J.J., Jalili, A., Kitajima, K., Kurokawa, H., McArthur, C., Lucas, P.W., Markesteijn, L., Pérez-Harguindeguy, N., Poorter, L., Richards, L., Santiago, L.S., Sosinski, E.E., van Bael, S.A., Warton, D.I., Wright, I.J., Joseph Wright, S. and Yamashita, N. (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, 14, 301–312. <https://doi.org/10.1111/j.1461-0248.2010.01582.x>
- Pearcy, R. W. (1983) The light environment and growth of C 3 and C 4 tree species in the understory of a Hawaiian forest. *Oecologia*, 58, 19–25. <https://doi.org/10.1007/BF00384537>
- Poorter, H. and Remkes, C. (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, 83, 553–559. <https://doi.org/10.1007/BF00317209>
- Poorter, L. (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct. Ecol.*, 13, 396–410. <https://doi.org/10.1046/j.1365-2435.1999.00332.x>
- Reich, P. B., Walters, M. B. and Ellsworth, D. S. (1992) Leaf Life-Span in Relation to Leaf, Plant, and Stand Characteristics among Diverse Ecosystems. *Ecol. Mono.*, 62, 365–392. <https://doi.org/10.2307/2937116>
- Reich, P. B., Tjoelker, M. G., Walters, M. B., Vanderkelen, D. W. and Buschena, C. (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and

low light. *Funct. Ecol.*, 12, 327–338. <https://doi.org/10.1046/j.1365-2435.1998.00208.x>

Shinzato, T., Taba, K., Hirata, E. and Yamamori, N. (1986) Regeneration of *Castanopsis sieboldii* [Fagaceae] forest, 1: Studies on stratification and age structure of a natural stand. *Sci. Bull. College. Agric. Univ. Ryukyus*, 33, 245–256. (in Japanese with English summary).

Tateno, M. and Taneda, H. (2007) Photosynthetically versatile thin shade leaves: A paradox of irradiance-response curves. *Photosynthetica*, 45, 299–302. <https://doi.org/10.1007/s11099-007-0049-6>

Thornley, J. H. M. (1976) *Mathematical models in plant physiology*. Academic Press, London.

Turnbull, M. H. (1991) The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. *Oecologia*, 87, 110–117. <https://doi.org/10.1007/BF00323788>

Valladares, F., Allen, M. T. and Pearcy, R. W. (1997) Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. *Oecologia*, 111, 505–514. <https://doi.org/10.1007/s004420050264>

Veneklaas, E. J. and Poorter, L. (1998) Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. In Lambers, H., Poorter, H. and

Van Vuuren, M. M. I. (eds.) “*Inherent variation in plant growth: physiological mechanisms and ecological consequences*”. Backhuys. Leiden, pp. 337–361.

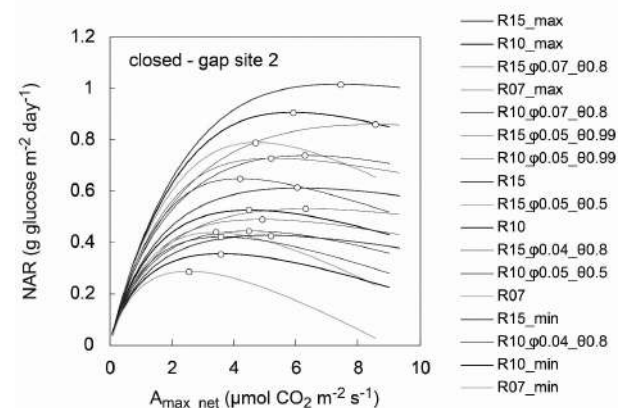
Walters, M.B., Kruger, E.L. and Reich, P.B. (1993) Growth, biomass distribution and CO₂ exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia*, 94, 7–16. <https://doi.org/10.1007/BF00317294>

Walters, M. B. and Reich, P. B. (1999) Low-light carbon balance and shade tolerance in the seedling of woody plants: do winter deciduous and broad-leaved evergreen differ? *New Phytologist*, 143, 143–154. <https://doi.org/10.1046/j.1469-8137.1999.00425.x>

Way, D. A. and Pearcy, R. W. (2012) Sunflecks in trees and forests: from photosynthetic physiology to global change biology. *Tree Physiol.*, 32, 1066–1081. <https://doi.org/10.1093/treephys/tps064>

Appendix Table 1. Photosynthetic capacities of leaves at ‘closed-gap patch 2’ after the typhoon disturbances.

Closed-gap site 2	
Species	A _{max_net} (μmol CO ₂ m ⁻² s ⁻¹)
<i>Ardisia crenata</i>	2.1
<i>Bredia okinawensis</i>	3.2
	3.3
	1.6
<i>Castanopsis sieboldii</i>	4.1
	5
<i>Cinnamomum doederleinii</i>	3.3
<i>Cinnamomum yabunikkei</i>	4.8
<i>Daphniphyllum teijsmannii</i>	5.1
	2.1
<i>Dendropanax trifidus</i>	3.9
<i>Elaeocarpus japonicas</i>	3.6
<i>Glochidion acuminatum</i>	8.2
<i>Hydrangea liukiuensis</i>	2.2
<i>Lasianthus fordii</i>	3.8
<i>Machilus thunbergii</i>	7.3
<i>Meliosma rigida</i>	3.5
<i>Psychotria asiatica</i>	2.3
<i>Pyrenaria virgata</i>	3.6
Mean ± SD	3.8 ± 1.7
A _{max_net} : a net value (i.e., A _{max} – leaf dark respiration rate)	



Appendix Fig. 1. An example of the calculated NAR for the understory sites.

Here the results of closed-gap site 2 (May–August 2012) are presented. Potential NARs are shown as several A_{max_net}–NAR curves each of them having different parameter set. A_{max_net} is A_{max} – R_d; R_d, leaf dark respiration rate. The curves show that NAR is maximal at a specific value of A_{max_net}. This is because, especially for a low-light environment, large values of A_{max_net} are ineffectual, but correspond to an increased R_d, which reduces NAR. In each panel, the legend indicates the line and its parameters set applied. Each parameter was changed separately, set at Φ = 0.04, 0.05 or 0.07 CO₂ mol quantum⁻¹, Θ = 0.5, 0.8, or 0.99, and R_d/A_{max} = 1/7, 1/10, or 1/15. ‘R10...’ represents R_d/A_{max} = 1/10 drawn by black lines, and ‘R15...’ and ‘R7...’ represent R_d/A_{max} = 1/15 and 1/7, drawn by gray lines and pale-gray lines, respectively. The standard bold lines labeled ‘R10’, ‘R15’ and ‘R7’ were drawn using (Φ, Θ) = (0.05, 0.8), those labeled ‘_max’ were using (Φ, Θ) = (0.07, 0.99), and ‘_min’ were using (Φ, Θ) = (0.04, 0.5), respectively. Solid thin lines represent Θ = 0.8, and dashed lines represent Θ = 0.5. The circles on each A_{max_net}–NAR curve shows the point at which NAR is maximized, and A_{max_net} is considered to be optimal.

弱光環境における個体の炭素収支と葉の機能的形質間のバランス： 沖縄亜熱帯林林床での研究

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要旨

本研究では、日本の亜熱帯林において、林床稚樹の葉の特性と個体の炭素収支との関連を調べ、弱光下で有利な形質について議論した。はじめに、複数の林床サイトにおいて光量子束密度を計測し、潜在的純生産量 (NAR) を推定した。次に、閉鎖林冠下の稚樹に対して葉の形質を調査し、著者ら開発の「葉に特化した相対成長率 (RGR_{leaf})」を用いて個体の炭素収支を推定した。 RGR_{leaf} は弱光下における個体の成長可能性を、葉面積当たりの乾燥重量 (LMA)、葉寿命 (LL)、葉への資源投資比 (LP) そして NAR のバランスから推定することができる。 $RGR_{leaf} > 0$ の場合、その個体は成長を続けていけると判定される。閉鎖林冠下の NAR 推定値は $< 50 \text{ g glucose m}^{-2} \text{ yr}^{-1}$ であり、このような光環境ではほぼすべての稚樹で $RGR_{leaf} \leq 0$ であると予測された。攪乱履歴のあるやや明るいサイトの NAR では、ほとんどの稚樹が正の RGR_{leaf} を持つと予測された。これらの NAR レベルにおいては、LMA、LL とともに RGR_{leaf} と相関関係は認められなかった。ただし LMA と LL には正の相関があり、一般に知られている関係に比べて LL に対する LMA の値が小さかった。一方、より明るいサイトの NAR では、小さな LMA および LL を持つもののほど RGR_{leaf} が大きくなると予測された。これらの結果から、弱光環境の林床における炭素収支の維持には、特定の葉の形質よりも形質間のバランスが重要であるといえた。台風攪乱によりもたらされる適度な暗さは、多様な葉の形質を持つ種の存在を可能にしていると考えられる。

キーワード：森林更新、葉寿命、葉面積当たりの乾燥重量 (LMA)、光環境、光合成、相対成長率、耐陰性

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