Photosynthetic acclimation, leaf turnover and growth in tree seedlings suddenly exposed to gaps in Jamaican montane rainforest

Tom Ball [ID] and Edmund Tanner [ID]

Department of Plant Sciences, University of Cambridge, Cambridge CB2 9EA, UK

Abstract

Mature leaves of tree seedlings were exposed to high light in four experimental gaps in the Jamaican upper montane rainforest (UMRF). Two of the six species studied were light-demanders: *Alchornea latifolia* and *Clethra occidentalis*. Two were gap-favoured: *Pittosporum undulatum* (an invasive) and *Palicourea alpina* (a subcanopy shrub). One was intermediate: *Hedyosmum arborescens*, and one was shade-tolerant: *Guarea glabra*. After five months, the following significant changes occurred in shade leaves that were exposed to gaps ('shade-to-gap' leaves; values as % of those in the pre-gap shade): maximum rate of photosynthesis + 40% (*Alchornea*), +35% (*Clethra*), −34% (*Pittosporum*), +72% (*Palicourea*); dark respiration +120% (*Alchornea*), +140% (*Clethra*), +60% (*Pittosporum*), +233% (*Palicourea*), +175% (*Hedyosmum*), +100% (*Guarea*); leaf thickness +18% (*Alchornea*), +18% (*Clethra*), +14% (*Palicourea*); leaf mass per unit area +18% (*Alchornea*), +15% (*Pittosporum*). Leaves produced in the gaps were (as a percentage of total live leaf number) 74% (*Alchornea*), 71% (Clethra), 50% (*Pittosporum*), 71% (*Palicourea*), 62% (*Hedyosmum*) and 50% (*Guarea*). Photosynthetic rates of leaves produced in the gaps were 53–120% higher than 'shade-to-gap' leaves. Overall, shade leaves on the three native, more light-demanding species (*Alchornea*, *Clethra* and *Palicourea*) showed photosynthetic acclimation, while the more shade-tolerant species (*Hedyosmum* and *Guarea* and *Pittosporum undulatum*) showed little acclimation in shade-to-gap leaves.

CAMBRIDGE UNIVERSITY PRESS

Introduction

Seedlings in the understorey, when suddenly exposed to much higher light, will have 'shade leaves' that are not adapted to the new light climate. When shade-grown seedlings or saplings are suddenly exposed to such conditions, for example, in a treefall gap, the overall response will be to replace shade leaves with 'sun leaves', but for the first few months, pre-existing shade leaves may be the main site of photosynthesis (Naidu and DeLucia 1997). The differences between shade leaves and sun leaves are well known. They include higher maximum rates of photosynthesis (A_{max}), dark respiration (R_d), leaf thickness (LT), N content and leaf mass per unit area (LMA) (Sims and Pearcy 1991, Newell *et al.* 1993, García-Núñez *et al.* 1995, Naidu and DeLucia 1997, Wu *et al.* 2018). Acclimation of the plant to the changed environment leads eventually to lower leaf area ratios and associated changes in morphology (Popma and Bongers 1988, 1991; Kitajima 1994; Claussen 1996; Bloor and Grubb 2004; Ishii and Ohsugi 2011). However, comparatively little is known about how the shade leaves adapt to sudden increases in light.

There have been many experiments where plants in pots grown in shade are suddenly exposed to gap light conditions, but very few where naturally occurring seedlings in forests are suddenly exposed. In some species, the shade leaves acclimate soon after the increased light is imposed (often after a short period of photoinhibition; Kamaluddin and Grace 1992, Lovelock *et al.* 1994, 1998, Huang *et al.* 2015). There are likely to be differences between natural seedlings in forests and seedlings grown in pots even if the same soil is used. For example, in tropical lowland rainforest in Australia, a comparison between pot-grown seedlings in 0.8% daylight with seedlings of the same species in nearby forest showed that leaf weight ratios and relative growth rates were all significantly lower in seedlings in the forest understorey (Bloor and Grubb 2003). Differences between forest seedlings and pot-grown seedlings may be partly due to the different nutrient availabilities in pots of different sizes. Soil volume restriction has effects on various plant responses that relate fundamentally to the reduction of photosynthesis per unit leaf area, based on a review of 65 studies by Poorter *et al.* (2012). In addition to differences due to soil nutrient availability, there may be differences due to light climate. Seedlings in the forest understorey experience variable light including sunflecks, whereas seedlings in greenhouses do not usually experience similar variations.

Of studies to date on the effect on tree seedlings of changing the light climate from understorey to gap light conditions, only two used seedlings in natural forest. The first, of eight species in Japanese temperate deciduous forest, showed that A_{max} of pre-existing leaves of six

species was higher 30 days post-gap compared to pre-gap and leaf mass per area was higher in three of these (Oguchi *et al.* 2006). In the second study, in the tropical lowland rainforest in Puerto Rico, only one of three species showed an increase in A_{max} in pre-existing leaves after a hurricane, the palm *Prestoea acuminata* (Wen *et al.* 2008). A third study grew plants in pots in the understorey of tropical forest in Panama and after two years moved the pots to a gap (Kursar and Coley 1999). One species (an *Ouratea*, with long-lived leaves) had increased A_{max} about 46 days after transfer to the gap, and the other species (a *Hybanthus* with shorter-lived leaves) did not show increased A_{max}. In addition to these three forest-based experiments, there are eight studies of tree seedling acclimation completed in shade houses or growth chambers. In these studies, there were a total of 27 species, of which 15 showed increased A_{max} following the transfer from low light to higher light (Bauer and Thoni 1988, Strauss-Debenedetti and Bazzaz 1991, Kamaluddin and Grace 1992, Newell *et al.* 1993, Turnbull *et al.* 1993, Yamashita *et al.* 2000, Cai et al. 2005, Oguchi *et al.* 2005).

There is also interest in physiological aspects of the acclimation ability of invasive species, linked to various field observations of their ability to outcompete the native trees and shrubs in both gaps and shade. Pattison *et al.* (1998) found greater acclimation ability of invasive compared with native species in Hawaii, which was further supported by the study of invasive Melastomataceae by Baruch *et al.* (2000). Yamashita *et al.* (2000) noted differences in acclimation performance between pot-grown seedlings of tree species native to the Ogasawara Islands compared with the non-native, invasive *Bischofia javanica*. It acclimated more effectively than the native mid-successional species with which it most closely competed due to the greater increase in A_{max} of shade leaves after transfer, greater production of new leaves and increase in relative growth rate. A summary and analysis of these and other studies, by Fridley *et al.* (2023), indicate that forest invasions may be enhanced by the efficient carbon gain of the invasive species that can allow persistence and reproduction in the understorey, plus the ability of existing understorey plants to adapt to gaps faster than the native species.

Thus, it seems likely that many species, including some invasives, will have seedlings that will increase rates of photosynthesis in pre-existing leaves when these leaves are suddenly exposed to high light due to treefalls or defoliation of canopy trees after major windstorms. However, the acclimation of these 'shade-to-gap' leaves on seedlings growing in tropical rainforest, as a result of actual increases in light, has only been demonstrated once for *Prestoea* in lowland rainforest in Puerto Rico defoliated by a hurricane and that was for a palm that has exceptionally long-lived leaves compared to dicotyledonous trees (Wen *et al.* 2008). In that study, the leaves of two dicotyledonous species, whose seedlings were naturally grown in the shade, did not show acclimation (Wen *et al.* 2008). Our research investigated whether leaves of seedlings of six dicotyledonous species growing naturally in the understorey in a tropical montane rainforest in Jamaica would acclimate after the tree canopy over these seedlings was experimentally removed.

Materials and methods

Study site and species

The forest lies just south of the crest of the Grand Ridge of the Blue Mountains in Jamaica at an altitude of 1570 m (Figure 1). The area is subject to frequent defoliating hurricanes. The site was in a 'Mull Ridge' forest type (Grubb and Tanner 1976, Tanner 1977). Sixty-five tree species are found in this forest. Our study focused on five common tree species and one shrub (*Palicourea alpina*). Two are light-demanders: *Alchornea latifolia* and *Clethra occidentalis*. Two are gap-favoured: *Pittosporum undulatum* (invasive) and *Palicourea*. One is intermediate: *Hedyosmum arborescens*, and one is shade-tolerant: *Guarea glabra* (Healey 1990, McDonald *et al.* 2003). *Clethra* has a tendency to establish on tree ferns (Newton and Healey 1989). *Pittosporum undulatum* is native to Victoria, Australia. It has been invading the forest for many decades and appears to be exacerbated by periodic hurricanes (Bellingham *et al.* 1995, 2005; Chai *et al.* 2012).

The six species are subsequently referred to by their generic names. Sizes of the seedlings and numbers of individuals in each treatment are in Table 1. Seedlings were all naturally occurring; potting and transplantation were not used in the experiment.

Canopy defoliation

Four gap and four adjacent understorey 10 × 10 m plots were established (Figure 1). All plots were south-facing with a slope angle of 10°–15° and were separated by a minimum of 40 m over ground. There was no sign of recent canopy disturbance and existing treefall, and other gaps were avoided. Within the four randomly chosen future gap plots, all leafy branches were removed from all trees over 5 m height. Additional branch removal along the solar arc outside the plots minimised diurnal interception of direct solar radiation by the canopy. The extra removal helped to simulate hurricane effects more accurately than a vertical-sided gap. The small size of the removed branches meant that they could be lowered to the ground carefully without damage to seedlings, and great care was taken to avoid such damage.

Photosynthetic photon flux density (PPFD) was measured in the open by a permanently installed sensor (Skye Instruments Ltd., Llandrindod Wells, UK), at Bellevue Peak, approximately 1.6 km east of the site. At ground level, it was measured by PPFD sensors made from silicon-blue photodiodes to the design of Biggs *et al.* (1971). These were calibrated against a manufacturer-calibrated sensor (Delta-T devices, Cambridge, UK) and found to have an accurate linear calibration (Ball 2001). A net of 30–35 sensors was placed randomly both before and after gap creation in the four gap plots and continuously in understorey plots. They were set to log every five seconds with one-minute integration, over a period of three to five days, which was statistically optimal (Ball 2001, Ch 2). PPFD in the gaps was between 22 and 39%, while that in the understorey was c. 3%, of the integrated diurnal PPFD above the canopy (Figure 2). Gaps were created in the following months: G1: January 1998; G2: February 1998; G3: April 1998; G4: September 1998.

Rainfall during the experiment was also measured at Bellevue Peak (Hafkenscheid 2000). The recorded rainfall was within 1 standard deviation of the mean rainfall at nearby Cinchona Gardens (1500 m) for each month (20th-century average), lower than average from April to July 1998, higher than average during November 1998 and marginally lower than average during January to March 1999 (Figure 3). The dry spells did not induce any visible plant stress conditions at the site (T. Ball, personal observation).

Seedling measurements

Measurements were made on all seedlings of each species in each plot, except in the case of *Guarea* for which, due to its abundance in the understorey, 15 individuals on each plot were randomly selected for measurement (Table 1). If a seedling died, its existing
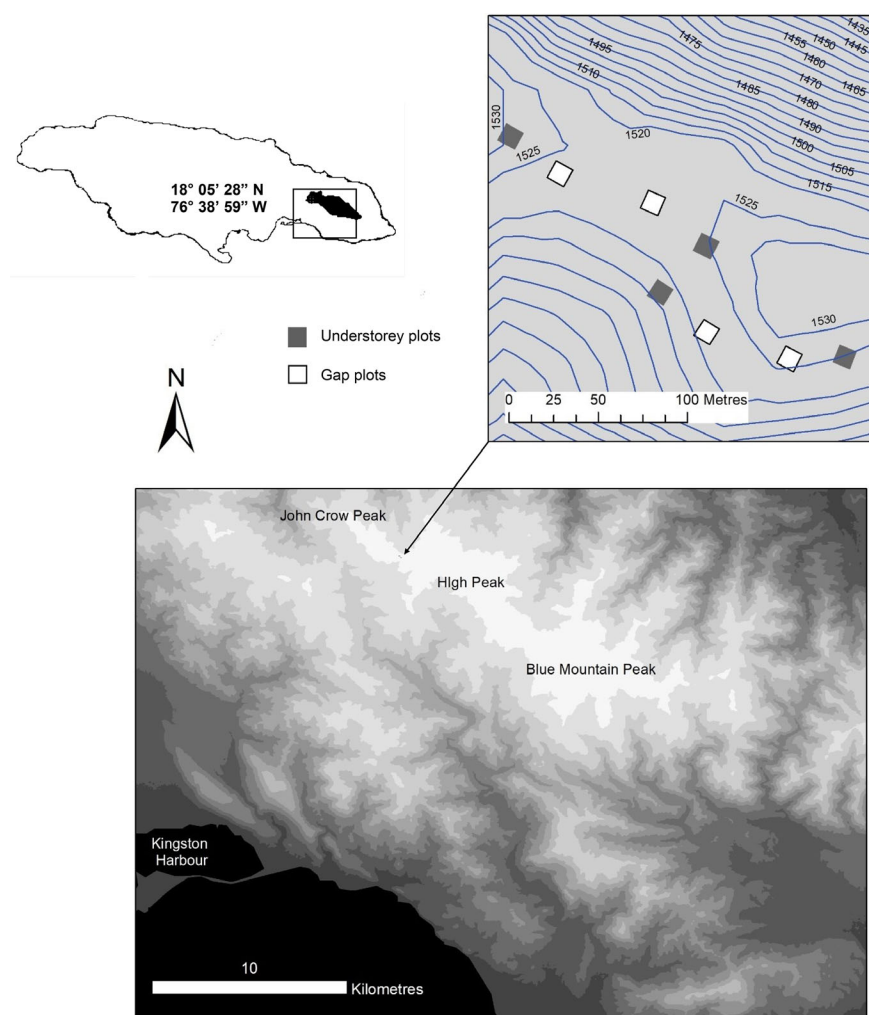
Figure 1. Study site and plot location. White band shows a 1500-m altitude contour.

data were eliminated from analyses; thus, the final data analyses were conducted only on the seedlings that survived the duration of the experiment.

Physiology

A_{max} and stomatal conductance (g_s) were measured simultaneously in saturating light, at about 700 µmol/m²/s. An infrared gas analyser (IRGA) was used in open mode with a Parkinson leaf chamber attached (LCA-2 with PLC-B, Analytical Development Company [ADC], Hoddesdon, UK). Equipment was supported by field retort clamps adjustable to each plant. Seedlings in the understorey were illuminated with a 50-W halogen lamp from which interception of infrared energy was neutralised by a small water film sandwiched between Lexan plastic filters. This shield admitted 90% of incident PPFD; PPFD values (saturating light, in gaps c. 1100–1500 µmol m⁻² s⁻¹) were measured below the shield by placing a small quantum sensor in the leaf position. In the gap, shading via mesh material filters reduced light progressively, with the infrared filter film preserved. Leaf temperatures (calculated by the LCA-2 from its own radiometer and internal calculations) were 20–25°C in the understorey and 22–28°C in gaps. All chamber and lighting equipment was carefully mounted and aligned by adjusting the clamp position so that the leaf was kept at a natural angle. CO_2 at the chamber inlet was stabilised by a 5-litre mixing volume and kept within ± 10% of ambient levels (app. 360–390 ppmv on the forest floor). Because this system had no chamber humidity control, a limited number of short replicate runs (generally 3–5) were carried out, keeping time in the chamber to approximately 40 seconds for each run. The minimum response time for this system is c. 30 seconds (ADC, LCA-2 manual). Measurements were taken in the morning hours between 8 a.m. and 12 noon, prior to any afternoon stomatal closure. R_d was measured after darkening the whole seedling for 20 minutes using a box. These measurements were made on separate days from the A_{max} and g_s. For consistency, measurements were made on the first fully expanded, non-self-shaded leaf from the top of each plant. While these were closely assessed for full expansion and maturity, the extent of maturity may have differed between plants. Following an A_{max} or R_d measurement, no further measurements were taken on the leaf for several subsequent days.

We use the following nomenclature: leaves in the shade before gap treatment are called 'shade leaves', the shade leaves that were exposed in the gaps are called 'shade-to-gap leaves', and new leaves produced in the gaps are called 'gap leaves'. A_{max} and g_s values were measured pre-gap on shade leaves and repeated on the shade-to-gap leaves at intervals that were as consistent as possible after gap creation on each gap plot (in practice 4–6 days, 14–16 days, 35–38 days and 63–66 days and 130–137 days after gap creation). R_d was

Table 1. Size, growth, survivorship (over the course of the experiment) and sample size of seedlings sampled in the study plots

Species	Height (cm)*	Growth rate (cm.yr-1)*		Survivorship (%)		Sample size							
		Gap	Understorey	Gap	Understorey	Gap				Understorey			
						G1	G2	G3	G4	U1	U2	U3	U4
Alchornea	27.5 (3.1)	4.3 (0.9)	0.8 (0.2)	59	78	4	3	11	7	11	15	4	7
Clethra	14.8 (2.4)	3.4 (0.8)	1.0 (0.2)	71	72	11	4	4	10	8	9	5	5
Guarea	18.1 (1.9)	1.7 (0.3)	0.7 (0.1)	59	95	15	15	15	15	15	15	13	15
Hedyosmum	26.3 (2.8)	2.3 (0.7)	1.4 (0.2)	79	84	1	7	5	6	8	15	5	4
Palicourea	18.3 (2.9)	2.9 (0.4)	1.1 (0.3)	68	77	6	5	4	5	5	8	6	6
Pittosporum	28.7 (3.9)	6.9 (1.1)	2.1 (0.2)	71	80	5	4	4	4	2	6	5	5

*Seedlings defined as < 30cm in height, measured from soil to top node.
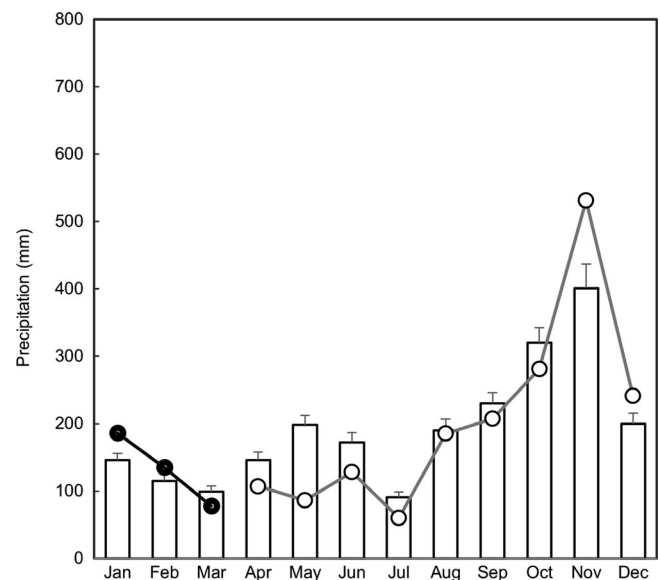Data ± 1 standard error of the mean in brackets.
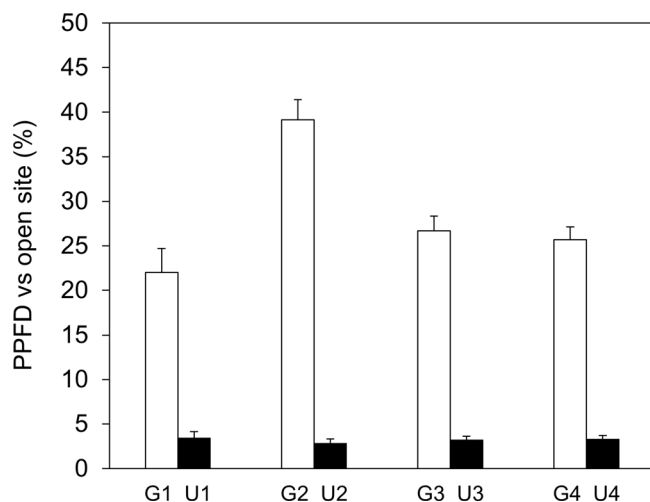
Figure 2. Average levels of diurnal integrated photosynthetic photon flux density (PPFD) in the study plots following gap creation. Columns represent means (± one standard error) of a network of sensors (30–40), randomly distributed in each plot and averaged over days, related to an open-site sensor on a nearby hilltop. Gap data were collected two to six months after the creation of the gaps. PPFD values in the open are typically 25–30 mol/m²/d (Hafkenscheid 2000).

Figure 3. Rainfall near the study site (Bellevue Peak) during 1998 (open circles) and 1999 (filled circles). The 20th-century averages are also shown (columns, error bars, 1 standard error) for Cinchona Botanical Gardens (data obtained from Jamaican Meteorological Service).

measured pre-gap and at 24–28 and 82–87 days. In understorey plots, A_{max} and g_s were measured twice (pre-gap and post-gap dates, termed 'pre-control' and 'post-control') and R_d once (pre-gap). The central point of each time interval following was taken for plotting data. A_{max}, g_s and R_d were measured on gap leaves once they had fully expanded, with expansion assessed by reference to existing mature leaves.

Leaf nitrogen concentration and leaf thickness

Following the final leaf census, the shade-to-gap leaf that had been measured for A_{max}, along with the uppermost sun leaf (if fully expanded), was excised. The corresponding leaves in the understorey seedling groups were also sampled and excised in the same way. Four to six 5 mm diameter discs were removed from the intervenous area of the leaf and dried (65°C for 12 hours). The discs were then weighed to determine leaf dry mass per unit area

(LMA). Leaf nitrogen concentration [N] was determined by the Kjeldahl method, using a Burkard scientific autoanalyser fitted with a colorimetric detector. LTs were measured with a dial micrometre, which did not compress the leaf, at six-week intervals. Measurements were taken at a minimum of six positions on either side of the midrib, between the side veins of the leaf.

Seedling growth and leaf demography

Seedling height was measured from ground level to the first fully expanded leaf from the top of the plant, before and six months after gap creation. Understorey plot seedling growth measurements were made at the start and end of 15 months of growth, in June to July 1997 and August to September 1998. For leaf demography, leaves were labelled using small wire loops on numerically tagged seedlings and recounted at intervals after gap creation.

Data analysis

Plot mean values were calculated for all leaf physiological variables (A_{max}, R_d and g_s) for each plot (gap and understorey). Individual species' mean values were then analysed for differences by the Mann–Whitney U (rank sum) test. Parametric tests were rejected owing to uncertainty about the normality of data distribution for the physiology data. These data sets were compared at two points in time: (1) at 4–6 days post-gap to pre-gap understorey and (2) gap measurement at 130–137 days post-gap (gaps) to five months in the understorey. LMA and LT data were compared between shade, shade-to-gap and gap leaves, again by Mann–Whitney U tests and also by regression of leaf [N] against shade, shade-to-gap and gap leaf A_{max}. All differences reported in the results were significant at the 0.05 level unless otherwise stated.

Leaf demography data were analysed for both the survivorship of the initial cohort present at gap creation and production of new leaves. Exponential fits were obtained to values of mean survivorship and mortality across all plots, and the exponential decay function was calculated according to the equations of Shiel et al. (1995). All statistical tests were performed using GENSTAT.

Results

Maximum photosynthetic rates (A_{max}) and dark respiration (R_d)

A reduction of A_{max} was observed in shade-to-gap leaves in four of the six species (the other two showed non-significant reductions) at four to six days after gap creation (Figure 4, Table 2); the reduction was particularly marked for *Pittosporum*, at -65%. However, by approximately 4.5 months post-gap, the shade-to-gap leaves showed significantly elevated A_{max} compared with their pre-gap levels in three species *Alchornea* (+40%), *Clethra* (+35%) and *Palicourea* (+72%). Stomatal conductance was only significantly elevated in one of these, *Palicourea* (+38%). *Guarea*, *Pittosporum* and *Hedyosmum* showed no significant photosynthetic acclimation of shade leaves.

Photosynthetic rates of gap leaves were significantly (53–120%) higher than in shade-to-gap leaves in all six species (Table 2, Figure 4). For those species that showed acclimation of shade leaves, the post-acclimation A_{max} values for shade-to-gap leaves remained significantly lower than those of the new 'gap' leaves in all cases (43–77%, Table 2). R_d rates also increased significantly in shade-to-gap leaves at 80–87 days post-gap (Table 2, Figure 4). Pre-gap understorey R_d ranged from –0.25 µmol m^{-2} s^{-1} (*Guarea*) to –0.39 µmol m^{-2} s^{-1} (*Palicourea*) but showed no significant trend according to the light demand of the species. Post-gap R_d in shade-to-gap leaves ranged from –0.56 µmol m^{-2} s^{-1} (*Guarea*) to –0.85 µmol m^{-2} s^{-1} (*Clethra*). Increases compared to the pre-gap rates were +120% (*Alchornea*), +140% (*Clethra*), +60% (*Pittosporum*), +233% (*Palicourea*), +175% (*Hedyosmum*) and +100% (*Guarea*). Sun leaf R_d was greater (more negative) than shade-to-gap leaf R_d for all species.

Leaf thickness (LT) and leaf mass per unit area (LMA)

In gaps, significant increases were seen in the LT of shade-to-gap leaves in the three species that showed photosynthetic acclimation (*Alchornea* +18%, *Clethra* +18% and Palicourea +14%; Figure 5). Only *Alchornea* and *Pittosporum* showed significant increases in LMA in shade-to-gap leaves (+18% and + 15%, respectively; Figure 6).

Leaf nitrogen concentrations

Leaf N concentrations ([N]) in understorey shade leaves ranged from 0.06 (*Clethra*) to 0.11 mg N cm^{-2} (*Guarea*, the most shade-tolerant species; Figure 7). Shade-to-gap leaves showed significantly increased leaf [N] over pre-gap values in only one species (*Clethra*, elevated by 23%). Gap leaf nitrogen was significantly higher than shade leaf N in all six species (Figure 7).

Interrelationships between leaf characteristics and A_{max}

A_{max} increased significantly with leaf N per area across the range of leaf types and species (Figure 8a). However, there was no significant relationship within the set of shade and shade-to-gap data; the significance of the relationships noted was down to the high [N] of gap leaves. Similarly, across all leaf types, A_{max} increased significantly with LT (Figure 8b), but the significance, as with the A_{max}–N relationship, was due to the higher values recorded for gap leaves and was not significant within the combined shade and shade-to-gap data set.

Leaf demography

All species showed pronounced elevation in rates of leaf production and leaf loss in gaps compared with the understoreys (Table 3). Leaf production was considerably lower than mortality immediately after exposure to high light but later increased to levels above mortality (Figure 9). The total number of leaves was higher at four to five months post-gap than in the same plants before gap creation; in two of the light-demanding species that showed acclimation of A_{max} (*Alchornea* 48% higher and *Clethra* 29% higher), increases in leaf numbers were lower for the other species (*Guarea* 11%, *Hedyosmum* 31%, *Palicourea* 8% and *Pittosporum* 14%). *Pittosporum* showed the lowest leaf mortality. Those seedlings with the lowest leaf production post-gap were also those that failed to increase their A_{max} in shade-to-gap leaves. By the end of the experiment, gap leaves constituted 74% (*Alchornea*) and 71% (*Clethra* and *Palicourea*) of the total leaves but only 62% for *Hedyosmum* and 50% for *Guarea* and *Pittosporum*.

Seedling growth and survivorship

In broad terms, seedling growth paralleled indications of photosynthetic acclimation (shade-to-gap leaf acclimation, gap leaf production, gap leaf photosynthetic rate and leaf nutrient status). Growth was faster in species that showed greater acclimation (Table 1). The greatest relative height growth rates (RGRs) were seen in the introduced *Pittosporum* (24% in gaps and 7% in understorey) and the two most light-demanding native trees (*Alchornea*, RGR 16% gap, 3% understorey and *Clethra*, RGR 23% gap and 7% understorey). Intermediate were *Palicourea* (RGR 16% gap and 6% understorey) and *Hedyosmum* (RGR 9% gap and 5% understorey), while the shade-tolerant *Guarea* showed the slowest overall RGR (9% gap, 4% understorey; figures for all RGR derived from Table 1). Seedling survivorship in gaps was lower than in the understorey for all species, varying between 59 and 71% of all seedlings (Table 1).

Discussion

In the Jamaican montane rainforest, shade leaves on seedlings suddenly exposed to higher light due to canopy defoliation above them increased their A_{max} in the two more light-demanding
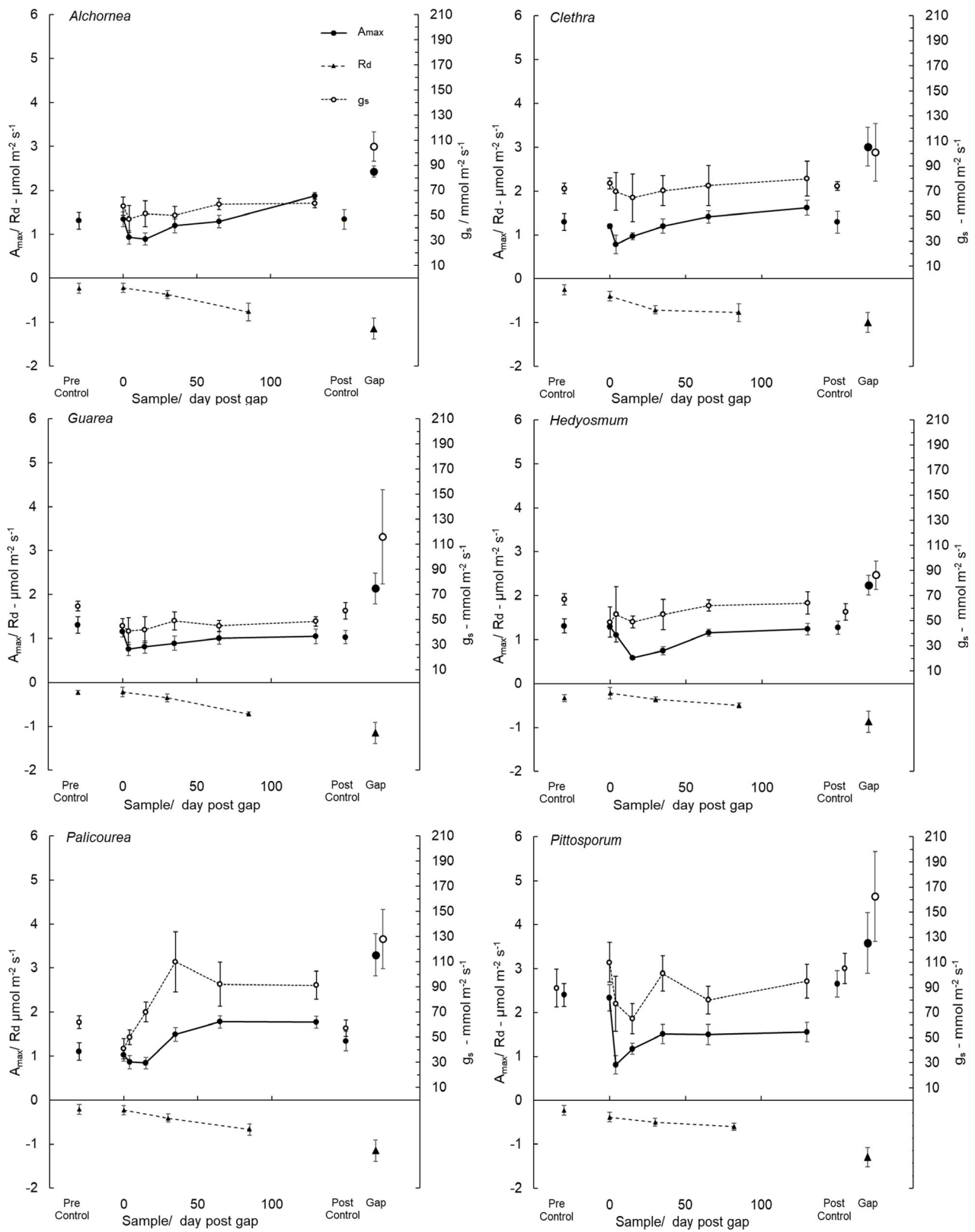
Figure 4. Leaf gas exchange characteristics during acclimation. Data points in the central part of each chart represent shade-to-gap leaves (present on seedlings before exposure of the leaves to high light). Data for leaves present on seedlings in understorey plots throughout the experiment are shown from pre- and post-gap samples. The right-hand part shows the data for fully expanded leaves that emerged after exposure to high light (gap leaves) with larger symbols. Point and error bars represent the mean and standard error across the study plots.

Table 2. Two sample comparisons (using Mann–Whitney U tests) for photosynthetic and respiratory parameters collected at intervals following the creation of canopy gaps. Sign indicates elevation (+) or depression (−) of the parameter compared to the control values

| | Shade-to-gap leaf to understorey comparison | | | | | Gap leaf to understorey comparison | | |
| | 4–6 days | | 130–137 days | | | 5 months | | |
	A_{max}	g_s	A_{max}	g_s	R_d	A_{max}	g_s	R_d
Alchornea	NS	NS	(+)*	NS	(+)*	(+)*	(+)*	(+)*
Clethra	(−)*	NS	(+)*	NS	(+)*	(+)*	NS	(+)*
Guarea	(−)*	NS	NS	NS	(+)*	(+)*	(+)*	(+)*
Hedyosmum	NS	NS	NS	NS	(+)*	(+)*	(+)*	(+)*
Palicourea	(−)*	NS	(+)*	(+)*	(+)*	(+)*	(+)*	(+)*
Pittosporum	(−)*	NS	(−)*	NS	(+)*	(+)*	NS	(+)*

*Significance at 0.05 level. NS indicates not significant. Tests were conducted on plot average values.

Table 3. Leaf mortality coefficients (calculated from the equations of Shiel *et al.* 1995) and percentage survivorship and production (mean ± 1 standard error of the mean) of leaves at six months following gap creation. Also shown are the computed exponential decay coefficient (λ) and the median leaf lifespan, both calculated from the equations of Shiel *et al.* (1995). See Figure 9 for gap leaf production and mortality graphs

| | Gap | | | | Understorey | | | |
| | 6-month post-gap % | | | | 6-month post-gap % | | | |
	Leaf survivorship	Leaf production	λ	Median leaf lifespan/year	Leaf survivorship	Leaf production	λ	Median leaf lifespan/year
Alchornea	39 ± 7.0	109 ± 5.8	1.63	1.24	77 ± 3.9	20.5 ± 5.4	0.34	3.5
Clethra	38 ± 4.3	91 ± 13.4	1.69	1.28	70 ± 12.5	21.2 ± 12.5	0.44	2.8
Guarea	55 ± 5.2	56 ± 12.9	1.06	1.53	97 ± 1.4	4.9 ± 2.4	0.16	6.8
Hedyosmum	26 ± 3.9	43 ± 9.2	2.55	1.09	78 ± 5.6	21.2 ± 5.0	0.40	3.0
Palicourea	26 ± 5.2	66 ± 3.3	2.31	1.11	87 ± 5.9	14.2 ± 6.6	0.32	3.7
Pittosporum	57 ± 4.7	57 ± 14.1	1.06	1.53	85 ± 7.2	20 ± 7.2	0.22	5.0
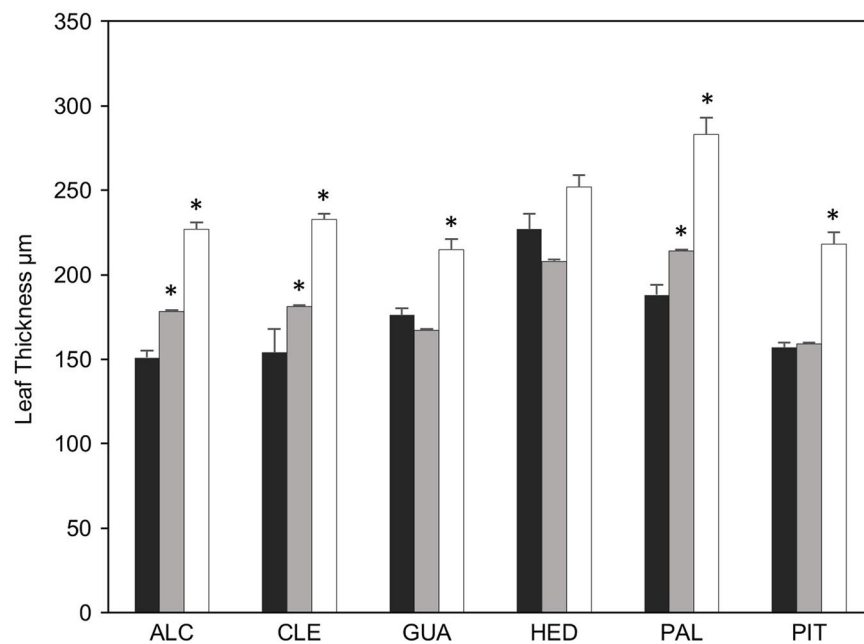
Figure 5. Leaf thickness of shade (black bars), shade-to-gap (grey bars) and gap (white bars) leaves at 150 days following gap creation. Shade leaves were taken from understorey plots. Asterisks indicate significant divergence from the species' shade leaf value (Mann–Whitney P > 0.05).
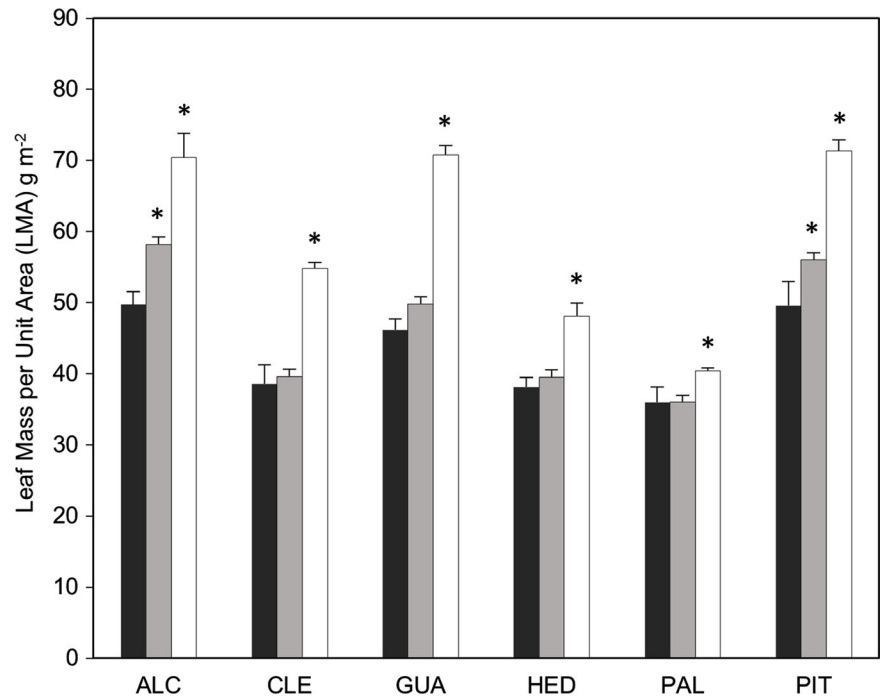
**Figure 6.** Leaf mass per unit area (LMA) at 150 days post-gap. Notation for leaf type as per Figure 5.
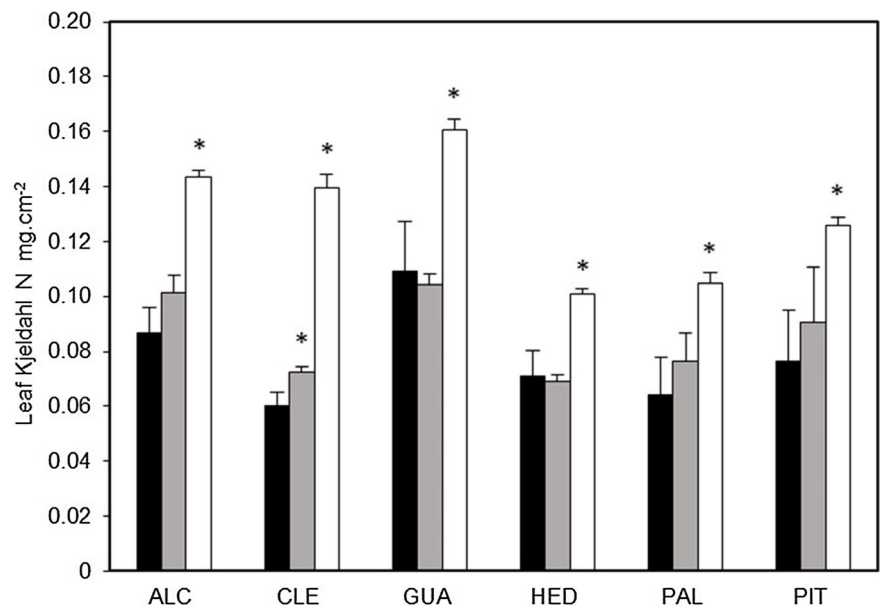
Figure 7. Area-based N concentration of leaves sampled and preserved at 150 days post-gap. Notation for leaf type and significance as per Figures 5 and 6.

species (*Alchornea* and *Clethra*) and the gap-favouring *Palicourea*, and in one species, *Clethra*, there were also increases in leaf mass per area and leaf N. Two more shade-tolerant species (*Guarea* and *Hedyosmum*) and the gap-favoured *Pittosporum* had lower or unchanged A_{max} in shade-to-gap leaves. This pattern of acclimation in shade leaves suddenly exposed to higher light was also seen in about half the species studied in other experiments. In the Japanese warm temperate rainforest, six of eight studied species of naturally occurring tree seedlings increased their A_{max} after sudden exposure to higher light following the creation of experimental gaps. The extent of the increase was similar among the six species and therefore unrelated to their relative light demand (Oguchi *et al.* 2017). In the semi-evergreen forest in Panama, of two shade-tolerant species, the one with long-lived

leaves showed increased A_{max} after exposure to a gap (Kursar and Coley 1999). In contrast, in a comparison of Australian rainforest species, the most light-demanding *Omalanthus* showed no acclimation when light levels were increased from 1% to 60%, whereas the mid-successional *Duboisia* and late successional *Acmena* did increase their A_{max} (Turnbull *et al.* 1993). Thus, more light-demanding species often, but not always, show increased A_{max} in shade leaves suddenly exposed to higher light.

The increase in A_{max} in shade-to-gap leaves in three Jamaican species was accompanied by increases in LT and in one species, *Clethra*, an increase in leaf mass per area and leaf N per area. In the only other study where leaf mass and leaf N were measured along with changes in A_{max} in shade-to-gap leaves (Oguchi *et al.* 2006), four of the six species that showed an increase in A_{max} also showed
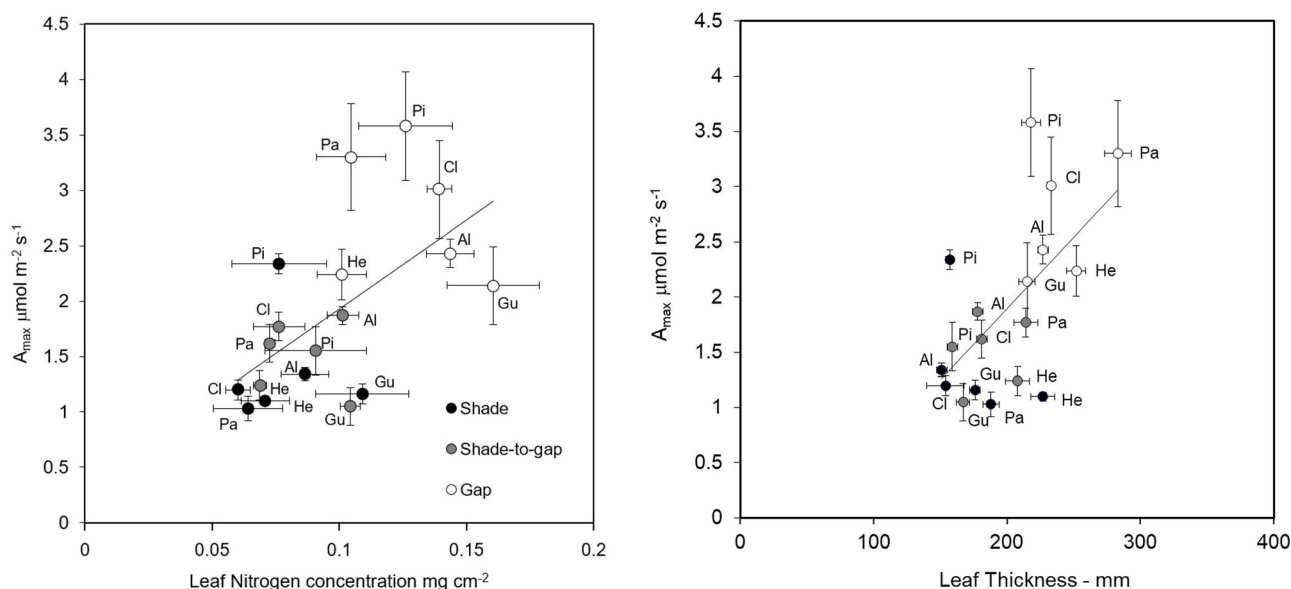
Figure 8. a. (Left panel) relationship between measurements of area-based leaf nitrogen content [N] and maximum photosynthetic rates (A_{max}) for all leaf types at approximately five months following exposure to the gaps. Overall regression across all leaf types for all species is significant: $A_{max} = 16.08$ [N] $+ 0.32$; $F = 8.621$, $P = 0.097$; $R2 = 0.35$; $n = 18$. b (Right panel) relationship between measurements of leaf thickness (LT) and maximum photosynthetic rates (A_{max}) for all leaf types at approximately five months following exposure to the gaps. Overall regression across all leaf types for all species is significant: $A_{max} = 0.013$ (LT) $+ 0.702$; $F = 9.39$, $P = 0.007$; $R2 = 0.37$; $n = 18$.

an increase in N, and three showed increases in leaf mass. Thus, it is common, but not universal, for increases in A_{max} in shade-to-gap leaves to be accompanied by increases in LMA and sometimes leaf N.
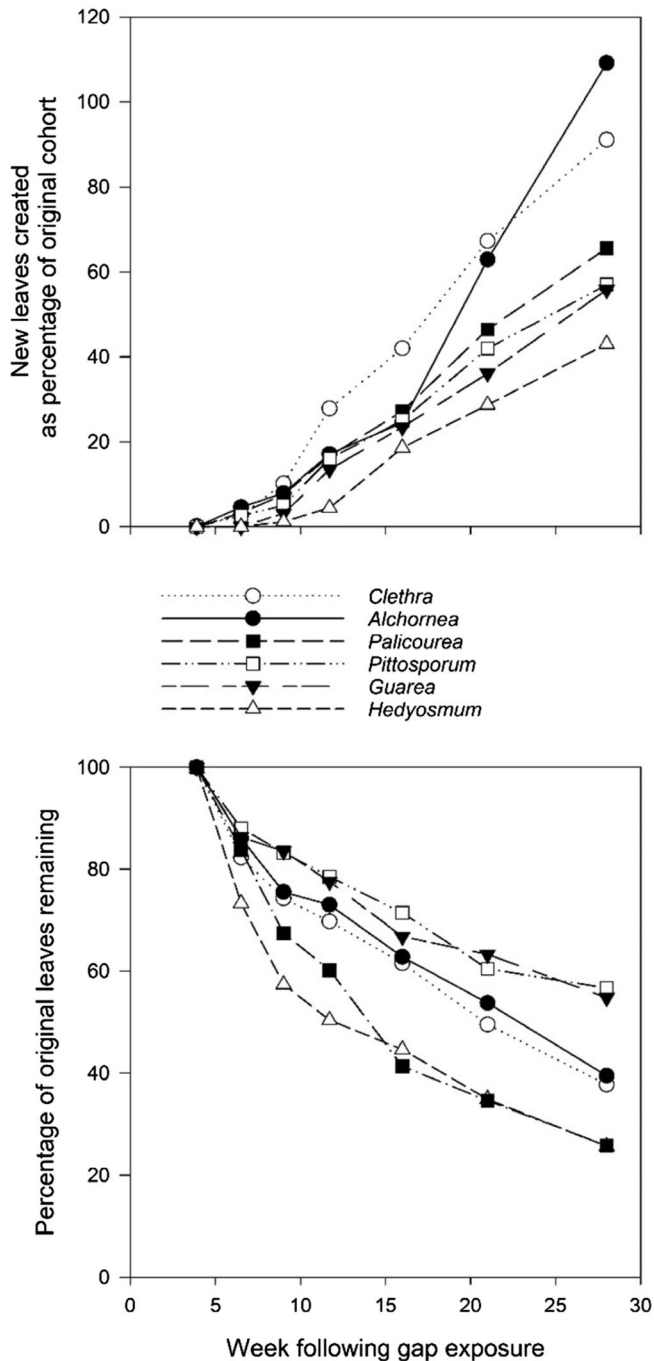
Leaf production following exposure to gap light in the Jamaican seedlings was higher over six months in all six species, including the three species where there was no increase in A_{max} in shade-to-sun leaves (Table 3). In Japan, seedlings of four of five subtropical evergreen trees showed significantly higher new leaf production in shade-to-gap plants compared to those that remained in shade (over one month in plants growing in a shade house, Yamashita *et al.* 2000). In a different Japanese experiment with eight species (different species to those in the Yamashita *et al.* 2000) in experimental gaps in warm temperate rainforest, few leaves expanded or died in 31 days after gap creation (Oguchi *et al.* 2006). In a study of two species in Panama, seedlings of *Hybanthus* transferred from shade to a gap, lost most of their leaves and 80 days later had 4.9 times as many leaves compared to when transferred. The second species, *Ouratea*, retained most of its pre-existing leaves and produced a few new leaves (Kursar and Coley 1999). Thus, seedlings of many species showed increased leaf production in shade plants suddenly exposed to gap light conditions; though the strongest and most rapid effects were seen in pot-grown plants in shade houses, naturally occurring seedlings in the forest showed no effect in a month after exposure to gap light (Oguchi *et al.* 2006) or took many months to produce new leaves (this study).

New leaf production was associated with increased A_{max} in shade-to-gap leaves in our Jamaican study and in two other studies: in the five species of Japanese subtropical evergreen trees suddenly exposed to gap light conditions in a shade house experiment (Yamashita *et al.* 2000) and in the six species of subtropical trees and shrubs in a shade house experiment in China (Cai *et al.* 2005). In contrast, the two species of Panamanian understorey shrubs studied in natural forest shade and gaps show different responses: one made new leaves, and the other retained its pre-existing leaves and

increased the A_{max} in those leaves (Kursar and Coley 1999). Thus, many, but again, not all, species show both increased A_{max} in pre-existing leaves and increased production of new leaves in new gap light conditions. While the invasive *Pittosporum* did not show an increase in A_{max} of shade leaves in this study, overall, it showed a high value for A_{max} in both shade and sun leaves despite its very low leaf LMA and leaf nitrogen. Consequent photosynthetic nitrogen use efficiencies are very high for this species; this underlies the very strong performance of this species in the understorey as well as the high growth rates noted in the gaps, a feature of invasive species that reflects high efficiency in carbon economics (Fridley *et al.* 2023).

Comparisons of experiments with naturally growing seedlings compared to experiments with seedlings in shade houses are not strictly possible because no study has compared the same species in these different conditions. However, a review of the published experiments suggests that plants in pots in shade houses respond more quickly than naturally occurring shade-grown seedlings suddenly exposed to gap light conditions. Shade house experiments report changes in only a month, whereas experimental gap studies either report increases in A_{max} or no increases in leaf production in a month (Oguchi *et al.* 2006) or a mixture of effects. A_{max} increased in a few weeks, but leaf production effects took many months to manifest themselves. In this study in Jamaica, there were few noticeable differences between species in new leaf production by five weeks after exposure to gap light, but they became clear by 26 weeks.

Full acclimation to gap light conditions will only have occurred once all leaves on a seedling were produced in the new light conditions, because even in species that do show increased A_{max} in pre-existing shade leaves, the increased A_{max} is not as high as the A_{max} in leaves produced in the gap light conditions (Figure 4 and Kursar and Coley 1999). In addition, pre-existing leaves survive for many months – in Jamaica, 26 weeks after the creation of gaps, the six species retained on average 41 % (range 27–57%, Figure 9) of their original leaves. The loss of old leaves and production of new ones is a continuous rather than sudden process in seedlings of most

Figure 9. Leaf production and mortality in the gap plots following exposure to high light. Error bars have been omitted for clarity, as have the data for survivorship and production in the understorey, which may be found in Table 3.

species even if adult trees show a markedly seasonal pattern of leaf production and abscission (Aylett 1985). No study has monitored seedlings until all leaves were produced in the new gap light conditions. Our Jamaican study seems to be the longest, but even here, only about half the pre-existing leaves were lost after six months. It would probably require at least one year for all pre-existing leaves to be lost (canopy leaves of large trees have an average lifespan of about one year [Aylett 1985]). In Panama, experiments would have needed to last many years since one of their species has leaves that typically last for five years (Kursar and Coley 1999).

Conclusion

Many, but by no means all, seedlings acclimate to being suddenly exposed to gap light conditions by increasing their A_{max} and sometimes increasing their leaf mass and leaf N in pre-existing leaves. Seedlings also produce new leaves in the new gap light conditions. Such changes start soon after the increased light is imposed and, in naturally occurring seedlings, can take many months and will not be fully achieved until all leaves on a seedling are produced in the gap light conditions. Some species show no increase in A_{max} in pre-existing leaves in the same conditions, whereas other species do show marked increases; one such species is the invasive alien *Pittosporum* in our Jamaican study, which only responds to a sudden increase in light by producing new leaves. Thus, seedlings growing in the low light of evergreen forest understoreys that are naturally exposed to much higher light after treefalls or wind defoliation of the canopy can respond by increasing photosynthesis in pre-existing leaves and by producing new leaves in the new light climate; acclimation of pre-existing leaves is presumably useful but is not necessary for a species to be successful. It is possible that a 'hump-shaped' response will eventually emerge when more species are investigated, with no increase in A_{max} for very strongly light-demanding and strongly shade-tolerant species, but those of intermediate light demand will show increased A_{max} in shade-to-gap leaves. In our study, the species that showed the most acclimation of A_{max} in pre-existing leaves and lower rates of shade leaf survival were the more light-demanding *Alchornea*, *Clethra* (canopy trees) and *Palicourea* (a subcanopy shrub); the three more shade-tolerant species, the introduced *Pittosporum* (which is successfully invading the native forests) and the native *Hedyosmum* and *Guarea*, showed no acclimation of shade leaves.

References

Aylett GP (1985) Irradiance interception, leaf conductance and photosynthesis in Jamaican upper montane rain forest trees. *Photosynthetica* **19**, 323–337.

Ball T (2001) Light Availability and Tree Seedling Ecophysiology in the Understorey of a Jamaican Montane Rainforest. Ch. 2 in Effect of Canopy Gaps on Tree Seedling Ecophysiology in a Jamaican Montane Rainforest. Ph.D. Thesis, University of Cambridge, Cambridge.

Baruch Z, Pattison RR and Goldstein G (2000) Responses to light and water availability of four invasive Melastomataceae in the Hawaiian islands. *International Journal of Plant Sciences* **161**, 107–118. https://doi.org/10.1086/314233

Bauer H and Thoni W (1988) Photosynthetic light acclimation in fully developed leaves of the juvenile and adult life phases of Hedera helix. *Physiologia Plantarum* **73**, 31–37. https://doi.org/10.1111/j.1399-3054.1988.tb09189.x

Bellingham PJ, Tanner EVJ and Healey JR (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* **76**, 2562–2580. https://doi.org/10.2307/2265828

Bellingham PJ, Tanner EVJ and Healey JR (2005) Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican

montane rain forests. *Journal of Vegetation Science* **16**, 675–684. https://doi.org/10.1111/j.1654-1103.2005.tb02410.x

Biggs WW, Edison AR, Eastin JD, Brown KW, Maranville JW and Clegg MD (1971) Photosynthesis light sensor and meter. *Ecology* **52**, 125–131. https://doi.org/10.2307/1934743

Bloor JMG and Grubb PJ (2003) Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology* **91**, 77–85. https://doi.org/10.1046/j.1365-2745.2003.00743.x

Bloor JMG and Grubb PJ (2004) Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. *Functional Ecology* **18**, 337–348. https://doi.org/10.1111/j.0269-8463.2004.00831.x

Cai Z-Q, Rijkers T and Bongers F (2005) Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. *Tree Physiology* **25**, 1023–1031. https://doi.org/10.1093/treephys/25.8.1023

Chai S-L, Healey JR and Tanner EVJ (2012) Evaluation of forest recovery over time and space using permanent plots monitored over 30 years in a Jamaican montane rain forest. *PLOS ONE* **7**, e48859. https://doi.org/10.1371/journal.pone.0048859

Claussen JW (1996) Acclimation abilities of three tropical rainforest seedlings to an increase in light intensity. *Forest Ecology and Management* **80**, 245–255. https://doi.org/10.1016/0378-1127(95)03606-7

Fridley JD, Bellingham PJ, Closset-Kopp D, Daehler CC, Dechoum MS, Martin PH, Murphy HT, Rojas-Sandoval J and Tng D (2023) A general hypothesis of forest invasions by woody plants based on whole-plant carbon economics. *Journal of Ecology* **111**, 4–22. https://doi.org/10.1111/1365-2745.14001

García-Núñez C, Azócar A and Rada F (1995) Photosynthetic acclimation to light in juveniles of two cloud forest tree species. *Trees* **10**, 114–124. https://doi.org/10.1007/BF00192192

Grubb PJ and Tanner EVJ (1976) The montane forests and soils of Jamaica: a reassessment. *Journal of the Arnold Arboretum* **57**, 313–368.

Hafkenscheid, RLLJ (2000) Hydrology and Biogeochemistry of Tropical Montane Rain Forests of Contrasting Stature in the Blue Mountains, Jamaica. Ph.D. Thesis, Vrije Universiteit, Amsterdam.

Healey JR (1990) Regeneration in a Jamaican Montane Tropical Rainforest. Ph.D. Thesis, University of Cambridge, Cambridge.

Huang W, Zhang S-B, Zhang J-L and Hu H (2015) Photoinhibition of photosystem I under high light in the shade-established tropical tree species *Psychotria rubra*. Frontiers in Plant Science 6, 801. https://doi.org/10.3389/fpls.2015.00801

Ishii H and Ohsugi Y (2011) Light acclimation potential and carry-over effects vary among three evergreen tree species with contrasting patterns of leaf emergence and maturation. *Tree Physiology* **31**, 819–830. https://doi.org/10.1093/treephys/tpr079

Kamaluddin M and Grace J (1992) Photoinhibition and light acclimation in seedlings of *Bischofia javanica*, a tropical forest tree from Asia. *Annals of Botany* **69**, 47–52. https://doi.org/10.1093/oxfordjournals.aob.a088305

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

Kursar TA and Coley PD (1999) Contrasting modes of light acclimation in two species of the rainforest understory. *Oecologia* **121**, 489–498. https://doi.org/10.1007/s004420050955

Lovelock CE, Kursar TA, Skillman JB and Winter K (1998) Photoinhibition in tropical forest understorey species with short- and long-lived leaves. *Functional Ecology* **12**, 553–560. https://doi.org/10.1046/j.1365-2435.1998.00235.x

Lovelock CE, Osmond CB and Jebb M (1994) Photoinhibition and recovery in tropical plant species: response to disturbance. *Oecologia* **97**, 297–307. https://doi.org/10.1007/BF00317318

McDonald MA, Hofny-Collins A, Healey JR and Goodland TCR (2003) Evaluation of trees indigenous to the montane forest of the Blue Mountains, Jamaica for reforestation and agroforestry. *Forest Ecology and Management* **175**, 379–401. https://doi.org/10.1016/S0378-1127(02)00132-9

Naidu SL and DeLucia EH (1997) Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. *Tree Physiology* **17**, 367–376. https://doi.org/10.1093/treephys/17.6.367

Newell EA, McDonald EP, Strain BR and Denslow JS (1993) Photosynthetic responses of *Miconia* species to canopy openings in a lowland tropical rainforest. *Oecologia* **94**, 49–56. https://doi.org/10.1007/BF00317300

Newton AC and Healey JR (1989) Establishment of *Clethra occidentalis* on stems of the tree-fern *Cyathea pubescens* in a Jamaican montane rain forest. *Journal of Tropical Ecology* **5**, 441–445. https://doi.org/10.1017/S0266467400003916.

Oguchi R, Hikosaka K and Hirose T (2005) Leaf anatomy as a constraint for photosynthetic acclimation: Differential responses in leaf anatomy to increasing growth irradiance among three deciduous trees. *Plant Cell and Environment* **12**, 916–927. https://doi.org/10.1111/j.1365-3040.2005.01344.x

Oguchi R, Hikosaka K, Hiura T and Hirose T (2006) Leaf anatomy and light acclimation in woody seedlings after gap formation in a cool-temperate deciduous forest. *Oecologia* **149**, 571–582. https://doi.org/10.1007/s00442-006-0485-1

Oguchi R, Hiura T and Hikosaka K (2017) The effect of interspecific variation in photosynthetic plasticity on 4-year growth rate and 8-year survival of understorey tree seedlings in response to gap formations in a cool-temperate deciduous forest. *Tree Physiology* **37**, 1113–1127. https://doi.org/10.1093/treephys/tpx042

Pattison RR, Goldstein G and Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* **117**, 449–459. https://doi.org/10.1007/s004420050680

Poorter H, Hler JB, van Dusschoten D, Climent J and Postma JA (2012) Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Functional Plant Biology* **39**, 839–850. https://doi.org/10.1071/FP12049

Popma J and Bongers F (1988) The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* **75**, 625–632. https://doi.org/10.1007/BF00776429

Popma J and Bongers F (1991) Acclimation of seedlings of three Mexican tropical rain forest tree species to a change in light availability. *Journal of Tropical Ecology* **7**, 85–97. https://doi.org/10.1017/S0266467400005137

Shiel D, Burslem DFRP and Alder D (1995) The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* **83**, 331–333. https://doi.org/10.2307/2261571

Sims DA and Pearcy RW (1991) Photosynthesis and respiration in *Alocasia macrorrhiza* following transfers to high and low light. *Oecologia* **86**, 447–453. https://doi.org/10.1007/BF00317615

Strauss-Debenedetti S and Bazzaz FA (1991) Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* **87**, 377–387. https://doi.org/10.1007/BF00634595

Tanner EVJ (1977) Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *Journal of Ecology* **65**, 883–918. https://doi.org/10.2307/2259385

Turnbull MH, Doley D and Yates DJ (1993) The dynamics of photosynthetic acclimation to changes in light quantity and quality in three Australian rainforest tree species. *Oecologia* **94**, 218–228. https://doi.org/10.1007/BF00341320

Wen S, Fetcher N and Zimmerman JK (2008) Acclimation of tropical tree species to hurricane disturbance: ontogenetic differences. *Tree Physiology* **28**, 935–946. https://doi.org/10.1093/treephys/28.6.935

Wu JW, Su Y, Wang JH, He Q, Qiu Q, Ma JW and Li JY (2018) Morphological and physiological acclimation of *Catalpa bungei* plantlets to different light conditions. *Photosynthetica* **56**, 537–548. https://doi.org/10.1007/s11099-017-0706-3

Yamashita N, Ishida A, Kushima H and Tanaka N (2000) Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. *Oecologia* **125**, 412–419. https://doi.org/10.1007/s004420000475