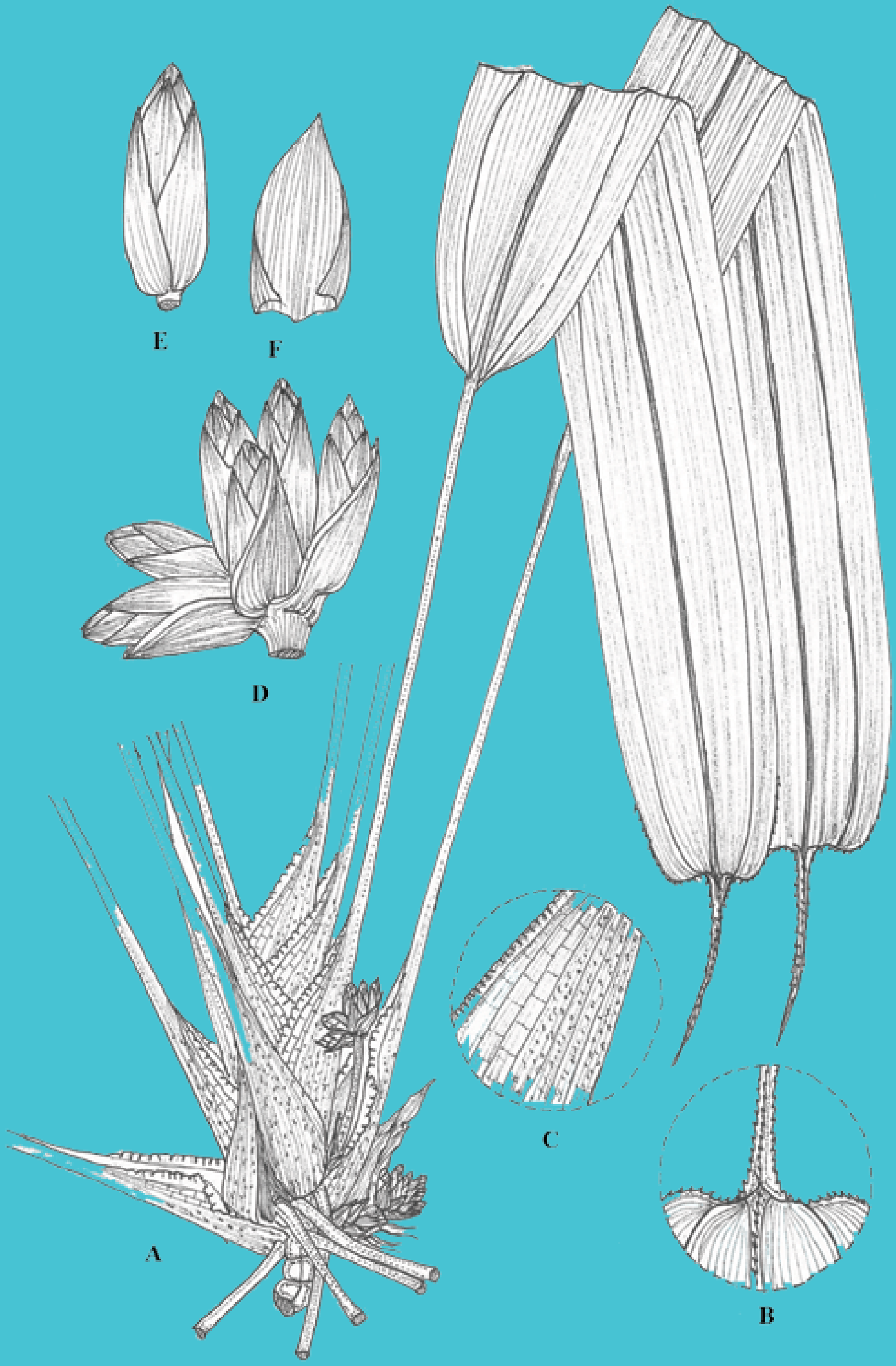
LIPI

REINWARDTIA

A JOURNAL ON TAXONOMIC BOTANY, PLANT SOCIOLOGY AND ECOLOGY

ISSN 0034 – 365 X | E-ISSN 2337 – 8824 | Accredited 792/AU3/P2MI-LIPI/04/2016



2016 15 (2)

REINWARDTIA

A JOURNAL ON TAXONOMIC BOTANY, PLANT SOCIOLOGY AND ECOLOGY

Vol. 15 (2): 67 – 135, December 22, 2016

Correspondence on editorial matters and subscriptions for Reinwardtia should be addressed to:
HERBARIUM BOGORIENSE, BOTANY DIVISION,
RESEARCH CENTER FOR BIOLOGY– INDONESIAN INSTITUTE OF SCIENCES
CIBINONG SCIENCE CENTER, JLN. RAYA JAKARTA – BOGOR KM 46,
CIBINONG 16911, P.O. Box 25 CIBINONG
INDONESIA
PHONE (+62) 21 8765066; Fax (+62) 21 8765062
E-MAIL: reinwardtia@mail.lipi.go.id
http://e-journal.biologi.lipi.go.id/index.php/reinwardtia

Cover images: *Mapania sembilingensis* Miraadila, Shabdin & Meekiong. A. Habit; B. Leaf apex details; C. Sheath margin details; D. Capitate inflorescence; E. Spike; F. Spicoid bract [Drawing by Meekiong, K.].

The Editors would like to thank all reviewers of volume 15(2):

David Simpson, Herbarium Kewense, Royal Botanic Gardens, Kew, UK
Herwasono Soedjito, Research Center for Biology, Indonesian Institute of Sciences, Bogor, Indonesia
Jay H. Bernstein, Robert J. Kibbee Library, Kingsborough Community College, New York, USA
Kuswata Kartawinata - Integrative Research Center, The Field Museum, 1400 Lake Shore Drive, Chicago, USA
Mark Hughes - Royal Botanic Garden Edinburgh, Edinburgh, Scotland, UK
Mien A. Rifai - Akademi Ilmu Pengetahuan Indonesia (AIPI), Indonesia
Siti Nur Hidayati - Middle Tennessee State University, Tennessee, USA
Soejatmi Dransfield - Herbarium Kewense, Royal Botanic Gardens, Kew, UK
Wong Khoon Meng - Singapore Botanic Garden, Singapore

REINWARDTIA
Vol 15, No 2, pp: 81 − 98

GROWTH RESPONSES OF PALM SEEDLINGS TO DIFFERENT LIGHT INTENSITIES STIMULATING CANOPY GAPS WITH AN ECOPHYSIOLOGICAL APPROACH

Received 16 February, 2016; accepted 22 September, 2016

DIAN LATIFAH
Center for Plant Conservation-Bogor Botanic Garden, Indonesian Institute of Sciences (LIPI) Jln. Ir. H.Juanda no. 13, Bogor, Indonesia 16122. Email: dian005@lipi.go.id

ROBERT A. CONGDON
College of Marine & Environmental Sciences, James Cook University, James Cook Drv, Townsville, Queensland, Australia 4811. Email: robert.congdon@jcu.edu.au

JOSEPH A. HOLTUM
College of Marine & Environmental Sciences, James Cook University, James Cook Drv, Townsville, Queensland, Australia 4811. Email: joseph.holtum@jcu.edu.au

ABSTRACT

LATIFAH, D., CONGDON, R. A. & HOLTUM, J. A. 2016. Growth responses of palm seedlings to different light intensities stimulating canopy gaps with an ecophysiological approach. *Reinwardtia* 15(2): 81 – 98. — Palms (Arecaceae) mainly grow in rainforests and many occur in disturbed areas like canopy gaps created by natural disturbances such as cyclones in Australia. Knowledge of seedling growth in different light intensities is essential to assist rainforest restoration in disturbed or marginal lands. The aim of this research was to investigate the effects of different light intensities on the seedling growth of *Arenga australasica* (H. Wendl. & Drude) S. T. Blake *ex* H. E. Moore, *Calamus australis* Mart., *C. moti* F. M. Bailey, *Hydriastele wendlandiana* (F. Muell.) H. Wendl. & Drude and *Licuala ramsayi* (F. Muell.) H. Wendl. & Drude. Seedling growth experiments (pot trials) were conducted in a glass house using shade cloth providing four different levels of shading: 59, 29, 17 and 6% sunlight. The growth rate, leaf turnover, leaf area, total chlorophyll, chlorophyll *a:b* ratio, vigor, above-ground and below-ground biomass and growth indices (LAR, SLA and LWR) of palm seedlings were measured. As a result of these measurements the relative shade tolerance of the five species was determined. The seedlings of *Arenga australasica* were classified as intermediate-shade intolerant species. *Hydriastele wendlandiana* seedlings were shade-intolerant. *Calamus australis* and *C. moti* seedlings are intermediate-shade intolerant. *Licuala ramsayi* seedlings were found to be a shade-tolerant.

Key words: growth, light, palms, restoration, seedling.

ABSTRAK

LATIFAH, D., CONGDON, R. A. & HOLTUM, J. A. 2016. Respon pertumbuhan semai palem terhadap variasi intensitas cahaya sebagai manipulasi kondisi bukaan kanopi dengan pendekatan ekofisiologi. *Reinwardtia* 15(2): 81 – 98. — Palem (Arecaceae) merupakan komponen utama di hutan hujan tropis. Banyak jenis palem tumbuh di hutan hujan tropis yang telah mengalami kerusakan dengan banyak bukaan kanopi seperti akibat bencana alam siklon di Australia. Pengetahuan tentang pertumbuhan semai pada kondisi intensitas cahaya yang berbeda sangat penting untuk diaplikasikan pada restorasi hutan dan lahan-lahan rusak yang terbuka atau marjinal. Tujuan dari penelitian ini adalah untuk mengetahui pengaruh berbagai intensitas cahaya terhadap pertumbuhan semai palem *Arenga australasica*, (H. Wendl. & Drude) S. T. Blake *ex* H. E. Moore, *Calamus australis* Mart., *C. moti* F. M. Bailey, *Hydriastele wendlandiana* (F. Muell.) H. Wendl. & Drude dan *Licuala ramsayi* (F. Muell.) H. Wendl. & Drude. Percobaan pertumbuhan semai dalam pot dilakukan di rumah kaca yang diberi paranet dengan empat tingkatan naungan yakni: 59, 29, 17 dan 6% cahaya. Variabel-variabel yang diamati meliputi kecepatan pertumbuhan, kecepatan pergantian daun, luas helaian daun, klorofil total, perbandingan klorofil *a/b*, vigor, biomasa dan indeks pertumbuhan tajuk dan akar, LAR, SLA dan LWC. Hasil menunjukkan kategori toleransi yang berbeda dari semai lima jenis palem terhadap naungan. Semai *Arenga australasica* serta rotan *C. australis* dan *C. moti* termasuk dalam kelompok jenis tidak tahan naungan tingkat sedang. Semai *Hydriastele wendlandiana* termasuk kategori tidak tahan naungan. Sedangkan *L. ramsayi* tergolong tahan naungan.

Kata kunci: cahaya, palem, pertumbuhan, restorasi, semai.

INTRODUCTION

Most palm species, in Australia, occur in rainforest habitats in northern Australia. Tropical cyclones are primary ecological drivers in northern Australia including north Queensland, as cyclones impact this region each year between November and May. Turton (2008) suggested that the rainforests in the region may be frequently affected by cyclones and become adapted to cyclonic disturbances. Cyclonic disturbance creates canopy gaps of differing size and various kinds of damage from minor stripping of foliage to large windthrows. Canopy gaps are important in promoting plant regeneration in most plant communities (Bullock, 2000).

Following cyclones that create canopy gaps, adult palms of several species flourish and their populations become denser. This is evident from studies of *Calamus australis* (Webb, 1958), *Licuala ramsayi* (Gorman, 1996), *Prestoea montana* (Frangi & Lugo, 1998) and *Archontophoenix alexandrae* (Dowe, 2009). Dransfield (1979) and Manokaran (1985) suggested that seedling of *C. manan* grows slowly in the understorey until a canopy gap is formed. Clearly, these studies show the importance of studying regeneration strategies with respect to the changing light environments in rainforests. However, seedling survival under varying light intensities is generally inexactly resolved for palm species.

Palm tree seedlings trap light to perform photosynthesis that produces biomass. In natural conditions, they have traits that enable them to adapt to a range of light environments from high to low light, reflecting the various habitats where they are found, from rainforest understoreys to the canopy or large gaps (Atwell *et al*., 1999). Therefore, their traits reflect their adaptive characteristics or responses to changing biotic or abiotic environment.

This research investigated the responses of palm seedlings under different light intensities based on the growth responses in both shade-tolerant and shade-intolerant plants found from previous studies. Specifically, the research determined the variations in the adaptive growth responses according to the tolerance of seedlings to levels of sunlight in the two extremes of (1) shade-tolerant, low-light tolerant or shade plants, and (2) shade-intolerant, high-light tolerant or sun plants (Poorter & Boot, 1998). Many plants exhibit intermediate states on the gradient between these two extremes (Atwell *et al.,*1999).

Plant adaptations are defined by Larcher (2003) in a broad perspective; these types of adaptation (which are not mutually exclusive) are: ‘modulative adaptations (functional flexibility)’, ‘modificative adaptations (phenotypic plasticity)’ and ‘evolutionary adaptation (genotypic plasticity)’. The latter, which, reflects ‘ecological differentiation’ as a result of ‘selection and adaptability’, results in plants adapted to dim-light, shade, intermediate light and strong-light (Larcher, 2003). Indeed, many plants tolerate a range of light environments (Anderson *et al.,*1988). ‘The reaction norm’ of a plant is genetically confined (Larcher, 2003) *i.e.* shade plants can adapt to high light intensities but not as well as the genetically adapted sun plants. The extent of tolerance reflects the presence of adaptive traits and these traits are expressed by competitors present at a site. The traits characteristics of shade and sun plants that contribute to species success in canopy gaps, which were examined in this study, are growth rate, leaf turnover, leaf area, leaf mass, allocation of resources to root or shoot biomass and chlorophyll content, including chlorophyll *a*:*b* ratio.

Sun plants can achieve faster growth rates than shade plants when light is not limited (Popma & Bongers, 1988). In this study, growth rate was determined as changes in seedling height over time. As palm seedlings lack stems, seedling height refers to the elongation of petioles and leaf blades. Dransfield (1979) and Manokaran (1985) found that the seedlings of *C. manan* grow very slowly in the rainforest understorey until a canopy gap forms, at which time the seedlings grow faster. The canopy gap formation can also be associated with local increases in nutrient levels (Chow *et al*., 1988). In another study, the height of seven rainforest tree seedlings (non palms) was lower under lower light intensities than those under higher light intensities (Poorter & Boot, 1998).

Sun plants may show faster turnover of leaves than shade plants. Poorter and Boot (1998) reported that the leaf turnover for tree seedlings of seven rainforest species (non palms) increased with light intensity. An experimental defoliation of *Sabal palmetto,* conducted by McPherson and Williams (1998), showed that young seedlings had large resources of carbon that allowed them to survive defoliation and periods of stress. Seedlings under a shady environment deal with the problem of predation (herbivory) by allocating an increased proportion of resources to defence (Larcher, 2003), including high leaf turnover, which decreases leaf longevity of some rainforest tree seedlings (Poorter & Boot, 1998).

Leaf area may be expected to increase in response to decreasing light availability and to increase the surface area for light interception for photosynthesis, as is evident in tropical-rainforest species such as *Amphitecna tuxlensis*, *Cecropia obtusifolia*, *Cordia megalantha*, *Myriocarpa longipes* and *Psychotria simiarum* (Popma & Bongers, 1988). However, non-palm rainforest tree species studied by Poorter and Boot (1998), *Cecropia* sp., *Schizolobium amazonicum*, *Cedrela odorata*, *Amburana cearensis*, *Astronium lecointei*, *Tetragastris altissima* and *Theobroma speciosum,* reduced their leaf area with decreasing light availability, as leaf area might have increased up to a point above which the required increase in leaf area for capturing limited light would not be efficient.

Plant traits such as total chlorophyll content and chlorophyll *a*:*b* ratios are exhibited in several ways under varying light intensities. Plants produce more chlorophyll *a* per unit mesophyll volume under high light intensity, for example in canopy gaps, in response to the increased availability of sunlight of high spectral quality (Chow *et al.,* 1988). Moreover, there is a tendency for shade-adapted plants to have relatively more chlorophyll *b*, relative to chlorophyll *a*, in response to the changed spectral quality in the understorey. Chlorophyll *a:b* ratios are species dependent; in general, the leaves of most green plants contain three times as much chlorophyll *a* as chlorophyll *b* (Raven *et al.,* 1999). The chlorophyll *a:b* ratio changes with changing light regime, reflecting changes in resource allocation to PSI and PSII of photosynthesis, as different chl *a:b* ratios are involved in each Photosystem (Raven *et al.,* 1999).

Leaf mass, above-ground biomass, below-ground biomass and root:shoot ratio were measured to examine resource allocation. Leaf mass is the dry weight of leaf blades; while above-ground biomass included both leaf blades and petioles (palm seedlings lack stems), which relates to the weight of total photosynthetic materials. The responses of biomass to different light intensities have been investigated in previous studies. An increase in light intensity can lead to increased leaf mass in some tropical rainforest trees (Popma & Bongers, 1988). However, the increase in leaf mass may decline in response to decreasing light availability (due to light competition under canopy gaps) where a further increase in leaf area would be uneconomic (Poorter & Boot, 1998). The root:shoot ratio reflects the allocation of resources: the energy, nutrient, support and water demands of the plant. These traits are related to water and soil nutrient uptake as canopy gaps can also be associated with local increases in nutrient levels (Lambers *et al.,* 1998).

Other growth indices considered in this study were leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR). LAR is the total leaf area of a plant divided by its dry weight (Atwell *et al.,* 1999). The ratio is useful because it relates total photosynthetic to total respiratory material, thereby giving information concerning the plant's available energy balance. An increase in LAR in response to a decrease in light intensity suggests that total photosynthetic material is more than total respiratory material in order to maximise harvesting light to undertake photosynthesis. SLA is the leaf area per unit dry mass of the leaves (Atwell *et al.,* 1999). Ten non-palm rainforest species exhibited lower SLA under more shaded conditions (Popma & Bongers, 1988), as in an environment where light is limited, it is an advantage to not increase leaf area more than required. SLA is an indirect measure of the return on investments in a productive organ. It is indirect as leaf dry mass costs per unit leaf area generally increase with leaf size; the return on investment (*i.e.* light capture) thus decreases as leaf size increases. This probably occurs because of the different biomass distribution between productive and support tissues in large, compared to small, leaves. However, the increase in leaf area is limited in an energy-limited system (*i.e.* limited light environment), where leaf area might increase up to a point above which the required increase in SLA would be uneconomic. LWR is the fraction of total plant weight allocated to leaves. The eudicot *Quercus pagoda* showed a high LWR under a small canopy gap with 27% sunlight or a shaded-environment with 8% sunlight (Gardiner & Hodges, 1998). This indicates that the proportion of biomass allocated to leaves is higher than the proportion of biomass distributed to the total plant.

Glass house trials on seedling growth in different light intensities were undertaken to investigate the effects of canopy gaps created in the field following cyclonic disturbance. The trials aimed to determine the effects of different light intensities on growth rate, leaf turnover, leaf area, total chlorophyll, chlorophyll *a:b* ratio, vigor, above-ground and below-ground biomass and growth indices (LAR, SLA and LWR) of palm seedlings.

The hypothesis tested is that growth responses vary between different species of palm seedlings under different levels of shade, and this reflects their adaptation to changes in light conditions caused by disturbance to the forest canopy. The varying growth responses reflect different survival strategies. Seedlings adapted to disturbance are predicted to grow better under higher levels of sunlight and will show features of shade intolerance, whilst species that are not adapted to disturbance will grow better under shade and show features of shade tolerance. However, there may also be species whose seedlings are adapted to a range of light intensities.

Palms adapted to a wide range of light intensities may allocate resources differently between the traits. It is, therefore, hypothesized that the growth responses will differ, reflecting different allocations of resources for survival strategies. Shade intolerant palms will show increased growth rates, vigor, chlorophyll content, chlorophyll *a:b* ratios and biomass under higher levels of sunlight, whilst shade tolerant species will show less of a decline in these variables under higher levels of shade.

MATERIALS AND METHODS

Location

The experiments were conducted using pot trials in a glass house located in the Douglas Campus of James Cook University, Townsville, from the fourth week of August 2008 to the first week of January 2010. The glass house was orientated north-south, and inside the average daily maximum temperature was 39.10 ± 0.63 ºC (Dry season, 33 readings) and 41.90 ± 1.40 ºC (Wet season, 32 readings); average minimum was

17.60 ± 1.40 ºC (Dry season, 33 readings) and 23.50 ± 0.84 ºC (Wet season, 32 readings) measured with a maximum-minimum thermometer over the full period of the experiment (the glass house is not climate-controlled so it has windows with wire-ventilations). The light levels inside the glass house, measured with a LICOR Quantum sensor when the sky was clear during midday, was 893 µmol quanta m^{-2} s^{-1} or 59% sunlight when compared to 1523 µmol quanta m^{-2} s^{-1} outside.

Materials

The five study species represent different growth habits and taxonomic groups: *Arenga australasica* (collection locality: Palmetum, Townsville); *Calamus australis* and *C. moti* (Tam O'Shanter/Djiru National Park, Mission Beach and Paluma); *Hydriastele wendlandiana* and *Licuala ramsayi* Tam O'Shanter/Djiru National Park, Mission Beach). The materials collected and used for this research were seedlings except *A. australasica*. The seedling stage was defined as the stage from the expansion of the first seedling leaf to when the leaves divided into 30 leaf elements (leaflets) or less and the height was 2.0 m or less. This definition is consistent with that of a related solitary palm, *Archontophoenix alexandrae* (Dowe, 2009). The concept of what constitutes the seedling stage was also based on Tomlinson (1990) and Henderson (2002). Tomlinson (1990) described the vegetative and reproductive development of palms in five steps involving gradual and smooth transitions: embryo, seedling, establishment phase, mature/adult vegetative and mature/adult reproductive phases. Henderson (2002) considered the palm development phases to be the seedling phase, juvenile phase and reproductive phase. Both agree that the seed phase, which may include seed dormancy, should not be considered as a developmental phase. The experiment starting date varied between species depending on the size of the seedlings. They were placed on one bench (28% sunlight) to allow them to acclimate to the conditions and to develop to a uniform size. They were then placed on the treatment benches to begin the experiment. The seedlings of *A. australasica* obtained from sprouted seeds (and having 1 eophyll when the new sprouts were transplanted) were ready to be moved to the treatment benches when they had produced 2 - 3 eophylls. *C. australis* had 4 leaves with 4 - 6 leaflets, *C. moti* had 1 - 4 leaves with 4 leaflets, *H. wendlandiana* had 2 - 4 leaves with 2 bifid leaves and *L. ramsayi* had 2 eophylls. These four species were placed on the treatment benches when they produced at least one new shoot.

Plastic pots were 22 cm (height) × 15 cm (diameter) and the growth medium was a commercial sandy loam (Bedrock Landscaping Supplies (Qld) Pty Ltd). Commercial shade cloth with four different levels of shading were used for the light intensity treatments. PAR (Photosynthetically Active Radiation) was measured with a LICOR Quantum sensor under each level of shade for light treatments.

Research Methods

The light environment can be simulated under experimental conditions to simulate natural low and high light conditions. For example, Atwell *et al.* (1999) used three levels of light, weak (30 µmol quanta m^{-2} s^{-1}), medium (130 µmol quanta m^{-2} s^{-1}) and strong (535 µmol quanta m^{-2} s^{-1}), to examine growth responses to light in *Flindersia brayleyana* (intermediate), *Toona australis* (sun-loving) and *Argyrodendron* sp. and *A. trifoliolatum* (shade-adapted). They considered low light to be less than 100 µmol quanta m^{-2} s^{-1}, high light to be about 1000 µmol quanta m^{-2} s^{-1} and full sunlight to be about 2000 µmol quanta m^{-2} s^{-1}. Gardiner and Hodges (1998) used four different light intensities to investigate their effects on the growth of *Quercus pagoda*. Based on these previous studies, four different light intensities were used in order to reflect the variation in light intensities found in natural forests subject to different levels of disturbance: 59, 29, 17 and 6% relative to full sunlight, which were equivalent to 893 (high), 447 (medium to high), 265 (medium) and 99 (low) µmol quanta m^{-2} s^{-1} respectively.

A completely randomized research design for a glasshouse experiment was applied based on Gasperz (1991). The arrangement of the five study species (*A. australasica*, *C. australis*, *C. moti*, *H. wendlandiana*, and *L. ramsayi*) was randomized between the four shade treatments. The seedlings and the position of the treatment benches and five study species were randomised in the beginning of the experiment. The arrangement of the treatments was spaced so as to avoid shading from adjacent benches. The number of replicates in each experiment varied depending on seedling availability and survivorship during the acclimatisation period. For *C. australis* there was nine replicates; *C. moti* seven replicates and for the other study species 15 replicates in each treatment. As sufficient sprouted seeds of all species were not available from the separate germination experiments (Latifah *et al.*, 2014), seedlings were obtained from the fields (*C. australis*, *C. moti* and *L. ramsayi* were collected from Tam O'Shanter/Djiru National Park; *H. wendlandiana* was collected from Kurrimine Beach National Park) for all species except *A. australasica*.

Growth rate was quantified by determining the change in the seedling height over time. The seedling height was measured every three weeks. The height was measured by lifting the leaf upright.

Leaf turnover was measured as a leaf dynamic variable. The number of leaves produced and shed was recorded every three weeks. Thus, the leaf turnover is a rate coefficient indicating how fast senesced leaves were replaced by new leaves; defined by Poorter and Boot (1998) as 'the rate at which the leaf pool in the plant crown is replaced'. Leaf turnover (LT) was calculated as follows:

$$LT = \frac{CLP + CLL}{TL}$$

where,

CLP = the cumulative leaf production – the number of leaves produced during the experiment period;

CLL = cumulative leaf loss; the total number of leaves lost during the experiment period. In the current experiment coefficients ranged between 0 and 2. For instance, when the leaf turnover is 1, it demonstrates that when the seedling had shed one leaf, one new leaf was produced; and

TL = the total number of leaves, including the fully open productive leaves and leaves which had been dying or become senescent.

$$TL = CLP + L_{w1}$$

where,

L_{w1} = number of functional leaves at the beginning of the experiment.

The chlorophyll content was determined at the end of the experiment, according to the method of Marr *et al.* (1995). Three circular subsamples were excised from the youngest fully expanded leaf using a cork borer (diameter = 6.9 mm, total area = 112.2 mm^2). A minimum of 3 replicates were taken and weighed to determine mass (mg). Each sample containing three subsamples was ground with about 2 mL of ice-cold 80% acetone and a pinch of acid-washed sand. This sample was then transferred to a centrifuge tube, made up to 4 mL with acetone, then centrifuged at 5000 × g for 5 min. The absorbance at 645, 663 and 750 nm was determined in a spectrophotometer (SpectraMax Plus 384, M3 Molecular Devices). Background absorbance was corrected by subtracting the reading at 750 nm from each of the A_{663} and A_{645} readings, and these corrected absorbance readings were used for the following calculations:

Total chlorophyll (mg L^{-1}) = $20.2\ A_{645} + 8.02\ A_{663}$
Chlorophyll *a* (mg L^{-1}) = $12.7\ A_{663} - 2.69\ A_{645}$
Chlorophyll *b* (mg L^{-1}) = $22.9\ A_{645} - 4.68\ A_{663}$
Chlorophyll (mg $sample^{-1}$) = chlorophyll (mg L^{-1}) * (v/1000)

where v is leaf extract volume in mL

Chlorophyll (ng mm^{-2})=chlorophyll (ng $sample^{-2}$) / 112.2(mm^2)

Seedling vigor was assessed to determine whether they were either (1) vigorous or likely to survive, or (2) moribund and unlikely to survive. Seedlings were categorized as vigorous when the number of senesced leaves was less than 50% of total leaves. The assessment was made at the middle (after 35 weeks in *A. australasica*, 47 weeks in *C. australis* and *C. moti*, and 34 weeks in *H. wendlandiana* and *L. ramsayi*) and end of the experiment (70 weeks in *A. australasica*, 94 weeks in *C. australis* and *C. moti*, and 67 weeks in *H. wendlandiana* and *L. ramsayi*).

Vegetative biomass is accumulated in shoots (leaves and petioles in palm seedlings) and roots, as no significant stem biomass was produced during the course of the experiment. Leaf mass, leaf area, final above-ground and below-ground biomass, Leaf Area Ratio (LAR), Specific Leaf Area (SLA), Leaf Weight Ratio (LWR) and Root:Shoot Ratio (RSR) were determined at the end of the experiment from the harvested biomass.

Data Analysis

The effects of different treatments on the changes in seedling height over time, leaf turnover, vegetative biomass and chlorophyll contents were determined by computing the 95% Confidence Interval for the mean of population (μ):

$$\text{Mean} \pm [t(0.025,df)\times SEM]$$

The values from the equation above were plotted in graphs with the error bars corresponding to a 95% Confidence Interval. Only the significant treatment effects of light intensities on the changes in seedling height overtime are displayed in graphs for a clear presentation (Fig. 1).

To estimate the growth rate, regression analyses were used whenever the regressions were significant at the 95% confidence level ($p < 0.05$) (Miles & Shevlin, 2001; Steel & Torrie, 1980). SPSS version 17.0 was used for the analyses.

RESULTS

Vegetative growth

The palm seedlings showed distinct responses at varying periods of time (Fig. 1). *Arenga australasica* and *C. australis* grew better under intermediate light intensities (17 and 29% sunlight) (Fig. 1a & b). A faster growth rate was also shown by *C. moti* under 17% sunlight (Fig. 1c). *Hydriastele wendlandiana* grew more rapidly in higher light intensities *i.e.* intermediate to high light intensities, 17–59% sunlight (Fig. 1d). *Licuala ramsayi* grew better under low than high light intensities (Fig. 1e).

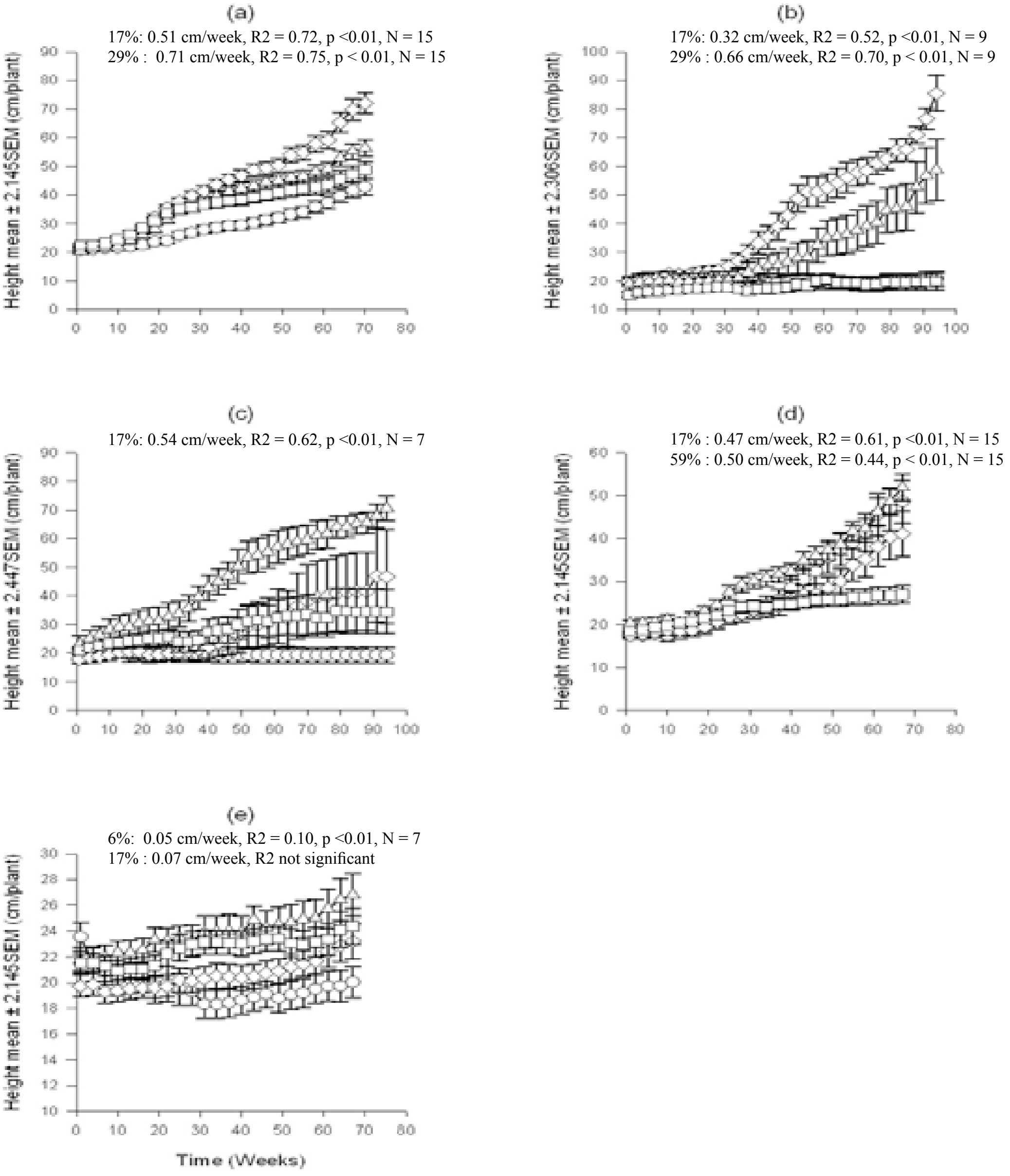


Fig. 1. The changes in seedling heights of (a) *A. australasica* over 70 weeks, (b) *C. australis* and (c) *C. moti* over 94 weeks, (d) *H. wendlandiana* and (e) *L. ramsayi* over 67 weeks under the 59 (○), 29 (◊), 17 (Δ) and 6 (□) % sunlight treatments. Values represent mean ± t×SEM. The significant differences at 0.05 levels are shown by non-overlapping error bars. The xy-axis captions are applied to all graphs.

Leaf turnover, leaf area and chlorophyll content

The palm seedlings responded differently under different light intensities as shown by their leaf turnover rates of 1.0–1.5 (Fig. 2). *Arenga australasica* showed low leaf turnover under lower light intensities, while *C. australis* decreased leaf turnover under higher light intensities. *Calamus moti* had a lower leaf turnover under 59% sunlight than the rest of the treatments. *Hydriastele wendlandiana* had the lowest leaf turnover under 17% sunlight. Leaf turnover of *L. ramsayi* was not significantly different between all treatments.

Leaf area varied under different light conditions (Fig. 3). The leaf areas of *A. australasica* and *C. australis* were smallest in the 6 and 59% light treatment. In the case of *C. australis* the difference between these two treatments and the intermediate ones (17 and 29%) appears significant. The lowest leaf area of *C. moti* was under 59% sunlight. Thus, the leaf areas are low under the highest (59%) light environments for *A. australasica*, *C. australis* and *C. moti*. In *H. wendlandiana* the leaf area under the highest light intensity was significantly greater than under the lowest. High variability of results meant that there were no significant responses under different light intensities in *L. ramsayi*; *C. australis* produced the

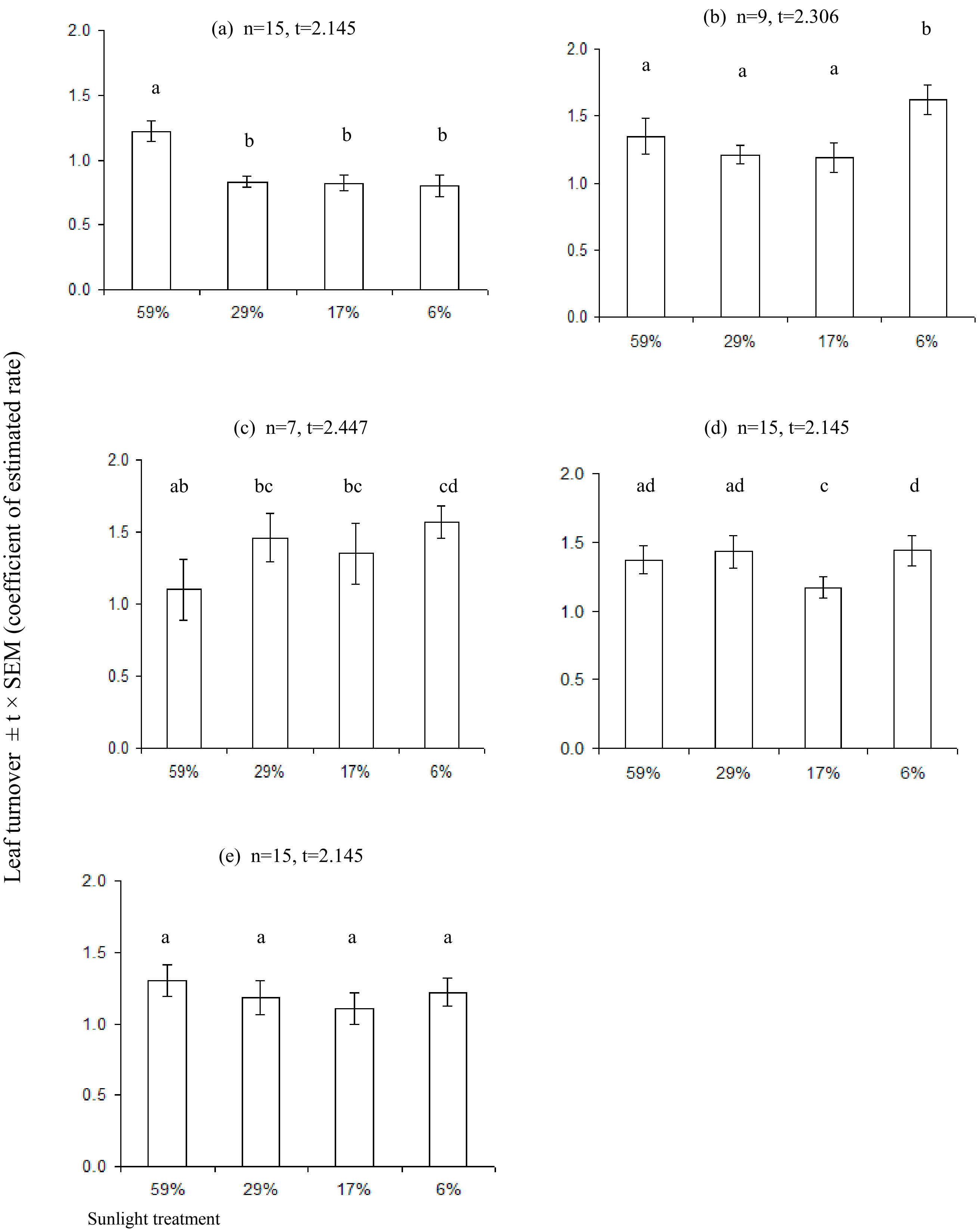


Fig. 2. Leaf turnover of (a) *A. australasica,* (b) *C. australis,* (c) *C. moti*, (d) *H. wendlandiana*, and (e) *L. ramsayi* under the 59, 29, 17 and 6% sunlight treatments. Values represent mean ± t × SEM, t depends on the number of replicates (n). Leaf turnover is a coefficient of estimated rate of shed leaves replaced by new leaves (scales= 0–2). Samples with the same lower case letters are not significantly different ($p = 0.05$). The xy-axis captions are applied to all graphs.

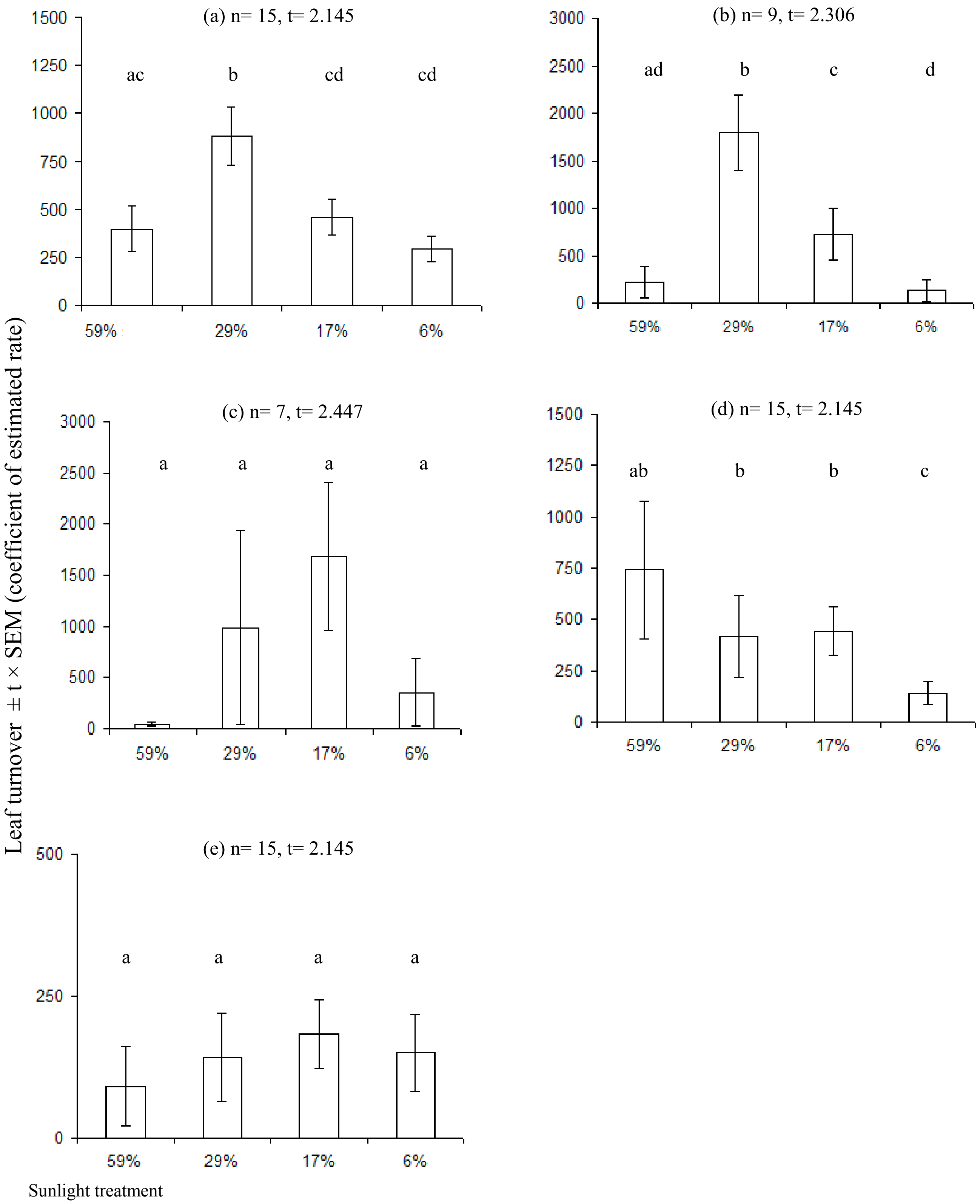


Fig. 3. Leaf areas of (a) *A. australasica,* (b) *C. australis,* (c) *C. moti*, (d) *H. wendlandiana* and (e) *L. ramsayi* under the 59, 29, 17 and 6% sunlight treatments. Values represent mean ± t × SEM, t values depend on the number of replicates (n). Samples with the same lower case letters are not significantly different (p = 0.05). The xy-axis captions are applied to all graphs.

greatest leaf areas (approximately 2,000 cm^2 per plant) under 29% light, while *L. ramsayi* produced the least (approximately 200 cm^2 per plant) under the same light condition.

The effects of light intensities on the chlorophyll contents of palm leaves at the end of the experiment varied under all light treatments in the five species, but there was high variability among replicates (Fig. 4). *Arenga australasica* had the highest chlorophyll content under higher light intensities. There was no significant difference in chlorophyll *a:b* ratios between treatments for each species.

Vigor

The vigor of the seedlings varied at different stages of the experiment, *i.e.* at the middle and end of the experiment (Table 1). Most seedlings (90-100%) of *A. australasica, C. australis, H. wendlandiana* and *L. ramsayi* were vigorous at the middle of the experiment. 80 to 100% of seedlings of *C. moti* were also classified as vigorous after 47 weeks, but only about 50% under the highest light intensity (59% light). Only seedlings of *A. australasica* remained vigorous (90-100% seedlings) at the end of the experiment. *Hydriastele wendlandiana* seedlings maintained their vigor under higher light intensities, while *L. ramsayi* maintained their vigor under lower light intensities. The seedlings of *C. australis* favoured intermediate light intensities. Almost half of *C. moti* seedlings were less vigorous at the end of the experiment (after 94 weeks), except those under 17% light.

Vegetative biomass

Leaf mass (the mass of leaf blades only) varied between the study species under different light conditions (Fig. 5). The overall responses of leaf mass were similar to those for leaf area. The leaf mass of *A. australasica* and *C. australis* was low under 59% light intensities. The results had high variability demonstrating that there were no significant responses under different light intensities in *C. moti*, *H. wendlandiana* and *L. ramsayi*. However, they showed some trends. The leaf mass of *C. moti* tended to be higher under intermediate light intensities and the lowest leaf mass of *C. moti* was under the highest light intensity (59% sunlight). *Hydriastele wendlandiana* tended to have higher leaf mass under higher light intensities.

As no stems were produced over the course of this experiment, above-ground biomass was comprised only of leaves and petioles (Fig. 5). The changes in above-ground biomass showed similar trends as those for leaf mass. *Arenga australasica, C. australis* and *C. moti* tended to yield low above-ground biomass under lowest as well as highest light intensities and was high at intermediate light levels. *Hydriastele wendlandiana* yielded most biomass under higher light intensities then declined under lower light. *Licuala ramsayi* tended to yield higher biomass when the light intensity was low.

The below-ground biomass was lower than above ground biomass, but showed similar trends (Fig. 5). There was little change in the below-ground biomass of *A. australasica,* while below-ground biomass tended to be lower under lower light intensities in *H. wendlandiana.*

Root:shoot ratios were not significantly influenced by the available light in this study, however there were some trends (Fig. 6). In *A. australasica*, *C. moti* and *H. wendlandiana*, the root:shoot ratios tended to decrease under the

Table 1. Vigor of five species of palm seedlings under varying light intensities

Species	n	Experiment stages	Vigorous seedlings (%) under each treatment 59%	29%	17%	6%
			sunlight			
A. australasica	15	Middle	100	100	100	100
		End	93	100	100	100
C. australis	9	Middle	90	100	100	90
		End	11	100	92	11
C. moti	7	Middle	56	88	100	90
		End	0	43	100	44
H. wendlandiana	15	Middle	100	100	100	100
		End	87	73	100	40
L. ramsayi	15	Middle	100	100	100	93
		End	40	73	93	79

Seedlings were assessed as being either (1) vigorous and likely to survive, or (2) moribund and unlikely to survive. Vigor is expressed as a percentage of the original number of seedlings (n). Seedlings were categorized as vigorous when the numbers of senesced leaves were less than 50% of total leaves.

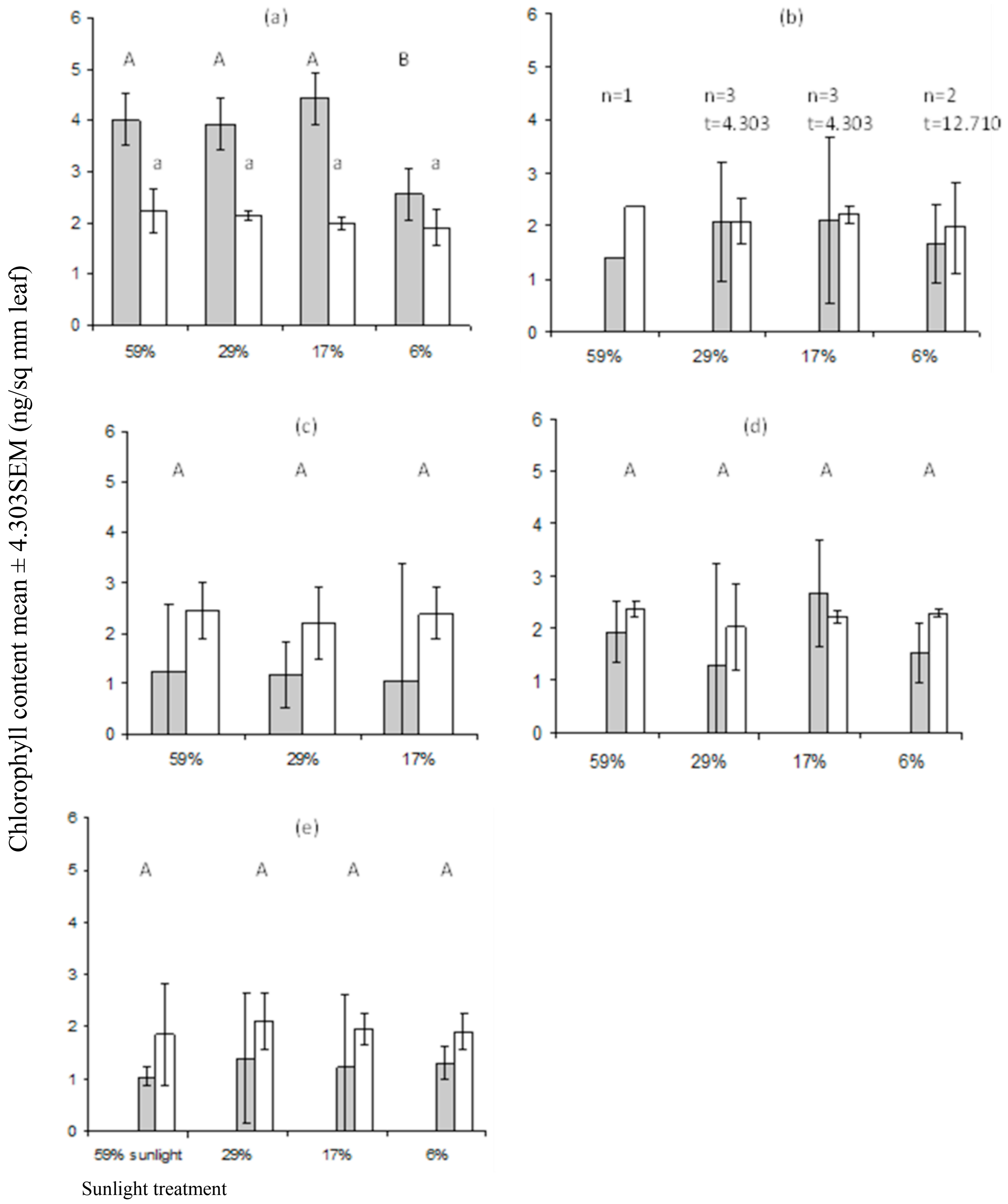


Fig. 4. Chlorophyll contents of *A. australasica* (a), *C. australis* (b), *C. moti* (c), (d) *H. wendlandiana* and (e) *L. ramsayi* - total chlorophyll (▨); ratio of chlorophyll a to b (□); Values represent mean ± (4.303 × SEM), n=3. Under 59% light there was only one *C. australis* with >50% green-portion of leaves, while there was insufficient leaf material for analysis in *C. moti*. Samples with the same lower/upper case letter are not significantly different (p = 0.05). The xy-axis captions are applied to all graphs.

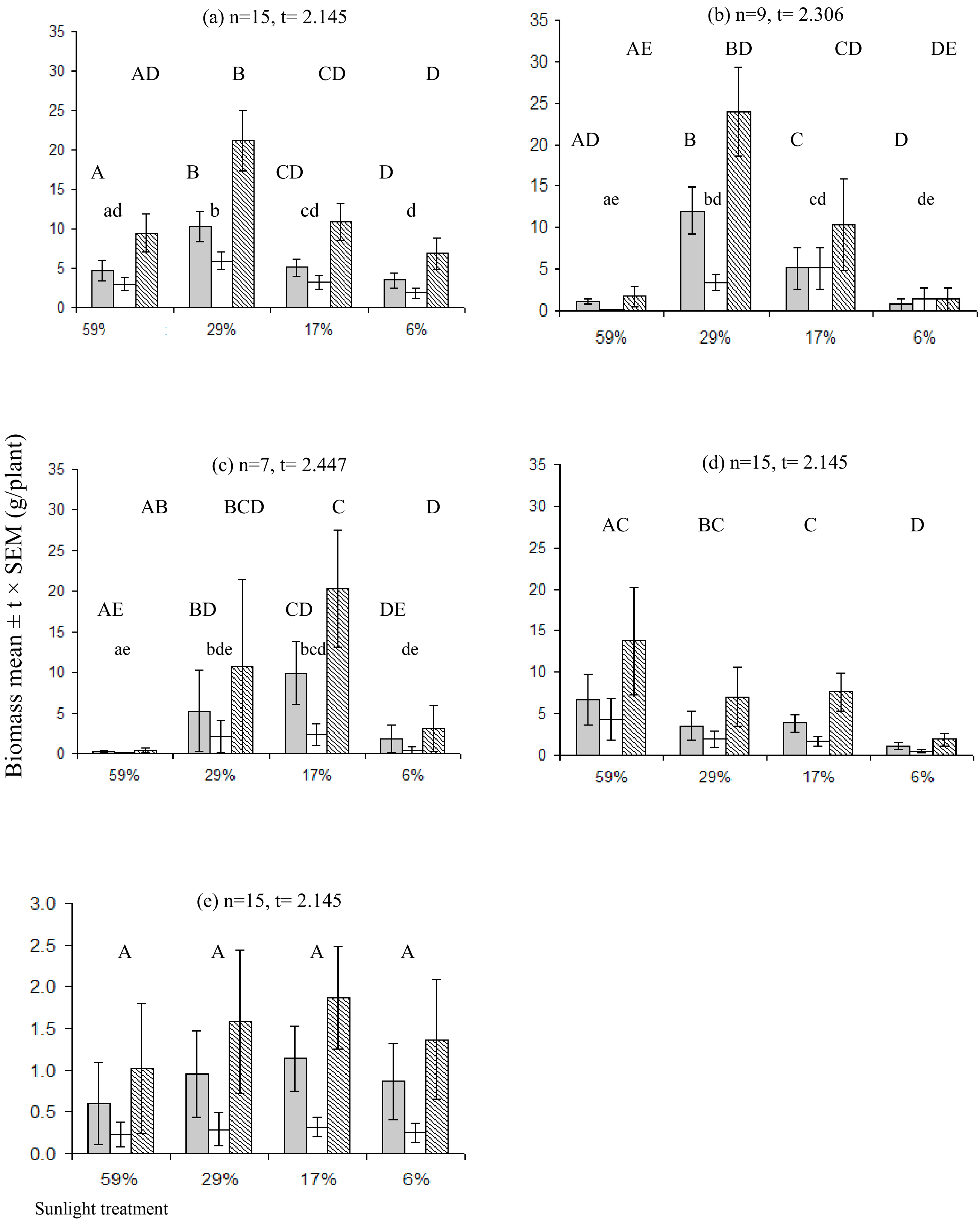


Fig. 5. Leaf mass (■), below-ground (□) and above-ground biomass (▨) of (a) *A. australasica,* (b) *C. australis,* (c) *C. moti*, (d) *H. wendlandiana* and (e) *L. ramsayi* under the 59, 29, 17 and 6% sunlight treatments. Values represent mean ± t × SEM, t values depend on the number of replicates (n). Samples with the same lower/upper case letters are not significantly different (p = 0.05). The xy-axis captions are applied to all graphs.

lower light intensities. That is relatively more leaves than roots were produced under lower light. In contrast, the root:shoot ratios of *C. australis* were higher under lower light intensities. In *L. ramsayi*, the highest root:shoot ratios were recorded under 59% sunlight but then there was a trend that the proportion of shoots slightly increased under lower light.

Overall, LAR of all species (Fig. 7) showed little difference between treatments except for *C. australis* and *C. moti*. *Calamus australis* had the highest LAR under the highest light intensities and *C. moti* had a low LAR under 17% sunlight. In addition, there were no clear trends in changes in SLA with treatments in all study species.

The leaf weight ratio (LWR, Fig. 7) also varied depending on the various light intensities. The LWR of *A. australasica*, *C. moti* and *L. ramsayi* were not significantly different and there are no clear trends. In *C. australis*, there was a trend that the LWR decreased under lower light intensities. *H. wendlandiana* tended to have higher LWR under 29% sunlight.

Responses to sun and shade inferred from five traits: growth rate, leaf turnover, leaf area, chlorophyll contents and biomass allocation

The seedlings of the palm species studied responded differently to varying light intensities (Table 2), in terms of growth rate, leaf turnover, leaf area, chlorophyll content, chlorophyll *a:b* ratio and below-ground biomass. These different responses were reflected in various responses of vigor and vegetative biomass.

Arenga australasica survived different light intensities, including the highest light intensities, by maximizing resource allocation to increased leaf turnover and decreased leaf area under 59% sunlight, and decreased total chlorophyll under 6% sunlight. Plants under 59% yielded more vigorous seedlings and vegetative biomass; while much lower biomass was produced under 6% sunlight. However, the seedlings under 6% were vigorous. This palm responded positively to the intermediate light intensities, 29 and 17% sunlight.

Calamus australis responded to 59% sunlight by decreasing leaf area and biomass, increasing its below-ground biomass under higher light intensities. This species increased leaf turnover in response to limited light. *Calamus australis* allocated proportionally more of its resources to above-ground parts, principally leaves, as indicated by the increased leaf mass and area under intermediate light intensities. Under 6% sunlight, increased leaf turnover, failed to maintain the vigor of the seedlings but more shoots and total plant mass were produced. Seedling growth was not inhibited under the 29 and 17% sunlight treatments.

Calamus moti responded to 59% sunlight by decreasing leaf turnover and leaf area. Under 59% sunlight seedlings were less vigorous and yielded more leaf mass and above ground biomass compared to those under 6% sunlight. Under 6% sunlight, increased leaf turnover maintained the plant vigor, and yielded a lower proportion of leaf mass. Under 29 and 17% sunlight, the palm seedlings showed positive responses in all the survival traits, but more biomass was produced under 17% than 29% sunlight.

Hydriastele wendlandiana dealt with 59% sunlight by investing in a higher seedling growth rate, increased leaf turnover and increased below-ground biomass. This species survived 6% sunlight with increased leaf turnover. Under 59% sunlight, seedlings maintained vigor and yielded maximum shoot and total plant mass; while, under 6% the seedlings became moribund with a greater proportion of root mass. The 29 and 17% sunlight treatments yielded maximum vegetative biomass.

Licuala ramsayi responded with increased leaf area under 59% sunlight; and increased seedling height and leaf area under 6%. Seedlings were vigorous and yielded maximum vegetative biomass under the highest and the lowest light treatments. Growth responses were positive under the 29 and 17% sunlight treatments.

DISCUSSION

The growth rates of the seedlings responded differently between species (Table 2). *Arenga australasica*, *C. australis* and *C. moti* grew better in intermediate than high or low sunlight (Figs 1a-c). *Hydriastele wendlandiana* grew more rapidly in intermediate to high light intensities (17–59% sunlight). *Hydriastele wendlandiana* grew fastest under the highest light treatment, and least in the low-light treatment. In contrast, *L. ramsayi* responded to decreased light with an increased growth rate. The relationship between growth rates were not significant in *L. ramsayi*. Popma and Bongers (1988) found that the heights of ten non-palm tropical rainforest species were not correlated with shade tolerance, *i.e.* the more shade-tolerant plants were not taller than shade-intolerant plants under low light. In contrast, even timber species studied by Poorter and Boot (1998) responded to competition for light by increasing their growth rate.

Leaf turnover of the palm seedlings responded differently under the different light intensities (Table 2). *Arenga australasica* responded to lower light intensities by lower leaf turnover. This suggests that this species survived the 59% sunlight treatment with increased leaf turnover. In contrast, the leaf turnover of *C. australis* had negative responses, or the leaf longevity of *C. australis* demonstrated positive responses, under high light intensities. *Calamus australis* survived

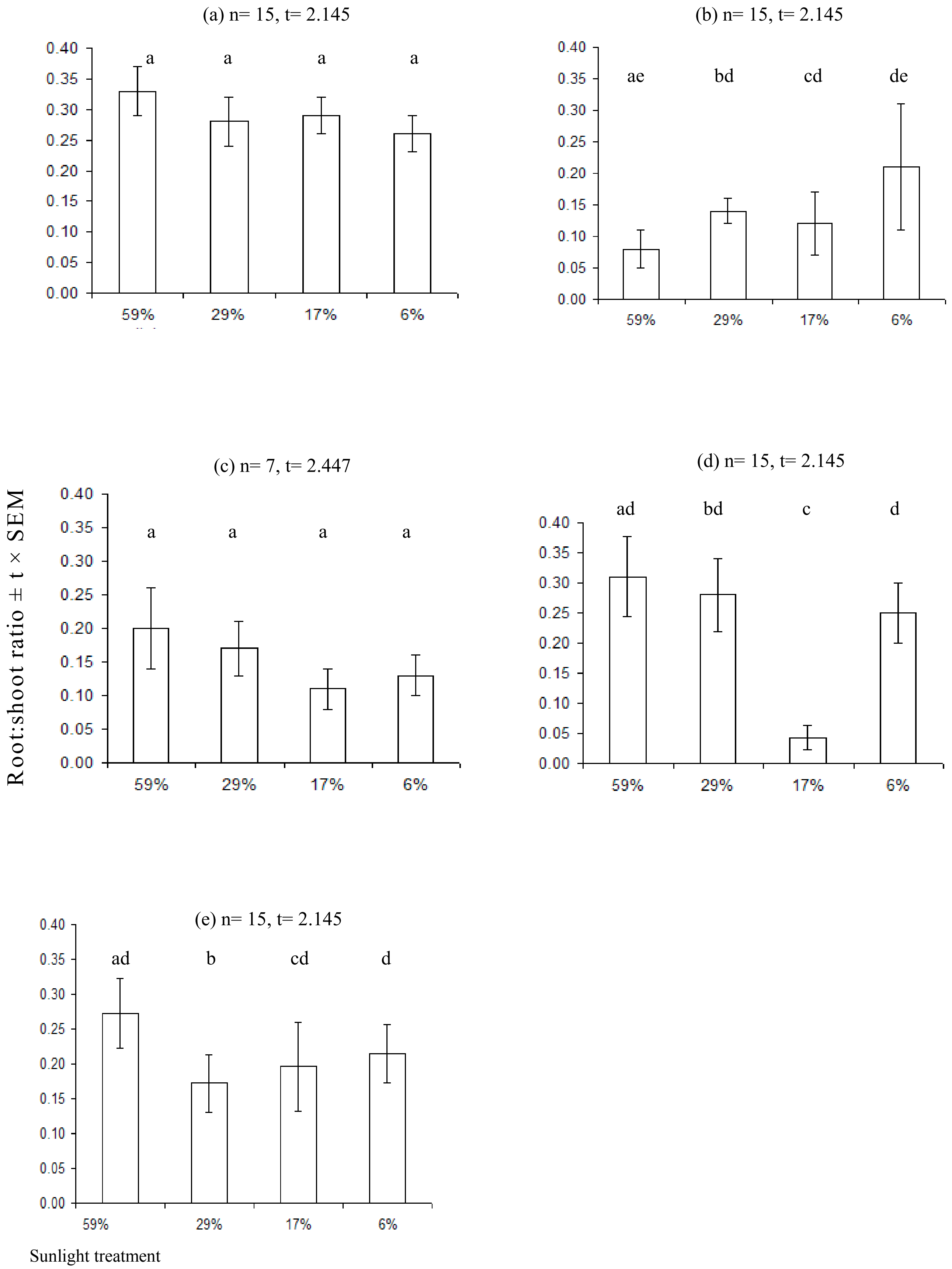


Fig. 6. Root:shoot ratios of (a) *A. australasica,* (b) *C. australis,* (c) *C. moti*, (d) *H. wendlandiana* and (e) *L. ramsayi* under the 59, 29, 17 and 6% sunlight treatments. Values represent mean ± t × SEM, t values depend on the number of replicates (n). Samples with the same lower case letters are not significantly different (p = 0.05). The xy-axis captions are applied to all graphs.

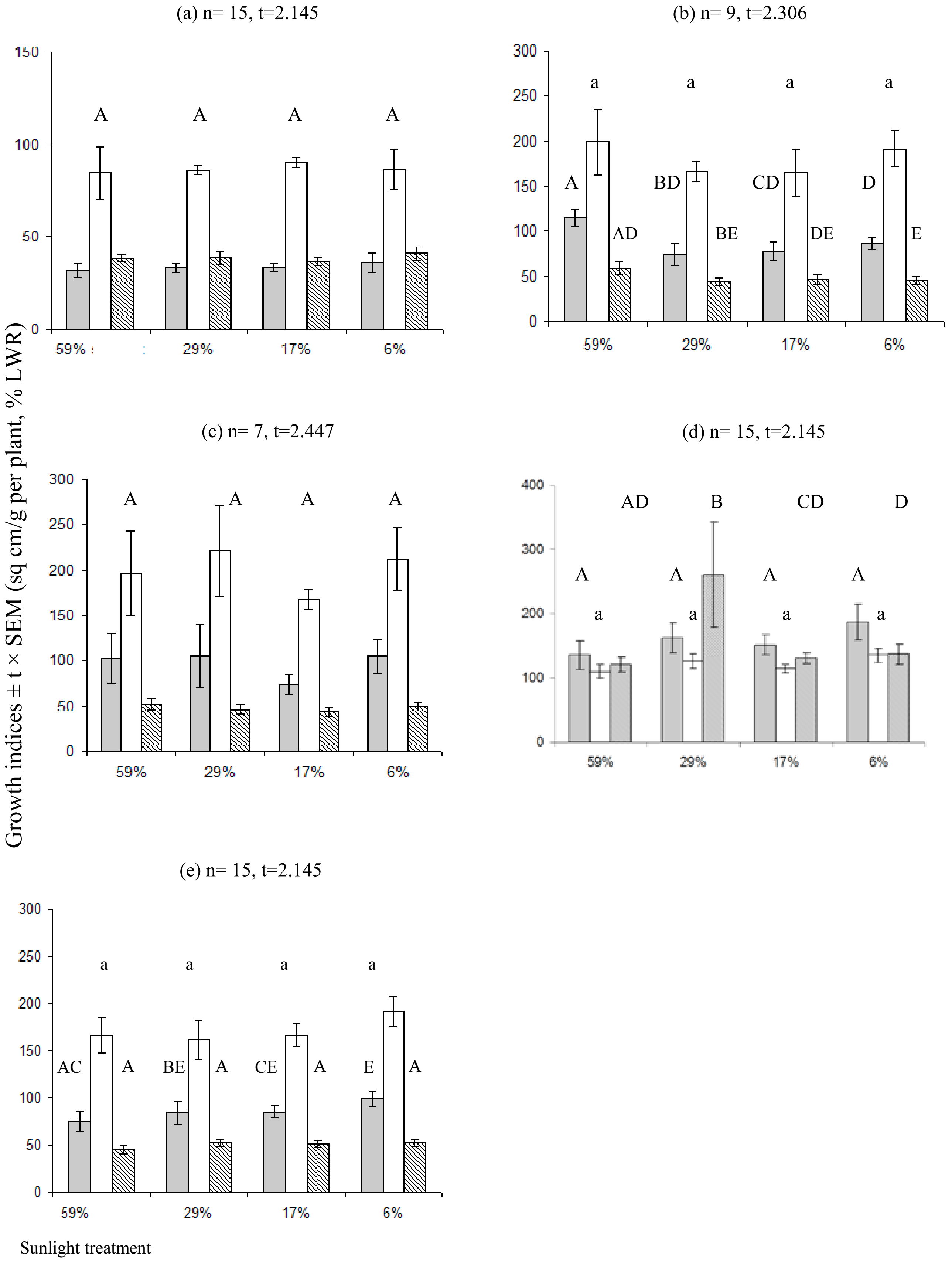


Fig. 7. LAR (■), SLA (□) and LWR (▨) of (a) *A. australasica,* (b) *C. australis,* (c) *C. moti*, (d) *H. wendlandiana,* and (e) *L. ramsayi* under the 59, 29, 17 and 6% sunlight treatments. The values of the original LWR is between 0–1; the values in the graph are expressed as % for clarity. Values represent mean ± t × SEM, t values depend on the number of replicates (n). Samples with the same lower case letters are not significantly different (p = 0.05). The xy-axis captions are applied to all graphs.

Table 2. Adaptation to sun and shade inferred from responses observed in this study

Responses	*A. australasica*					*C. australis*					*C. moti*					*H. wendlandiana*					*L. ramsayi*				
	59	29	17	6	S	59	29	17	6	S	59	29	17	6	S	59	29	17	6	S	59	29	17	6	S
Growth rate	-	+	+	-	IT	-	+	+	-	IT	-	+	+	-	IT	+	+	+	-	SI	-	+	+	+	ST
Leaf turnover	+	-	-	-	SI	-	-	-	+	ST	-	+	+	+	ST	+	+	-	+	SI	+	+	+	+	na
Leaf area	-	+	+	-	IT	-	+	+	-	IT	-	+	+	-	IT	not significant				na	not significant				na
Total chlorophyll content	+	+	+	-	SI	+	+	+	+	na	+	+	+	+	na	+	+	+	+	na	+	+	+	+	na
Chlorophyll *a:b* ratio	+	+	+	+	na	+	+	+	+	na	+	+	+	+	na	+	+	+	+	na	+	+	+	+	na
Vigor																									
Mid-experiment	+	+	+	+	na	+	+	+	+	na	-	+	+	+	IT to ST	+	+	+	+	na	+	+	+	+	na
End-experiment	+	+	+	+	na	-	+	+	-	IT	-	-	-	+	ST	+	+	+	-	SI	-	+	+	+	IT to ST
Leaf mass	-	+	+	-	IT	-	+	+	-	IT	-	+	+	-	IT	+	+	-	+	SI	-	+	+	+	ST
Above-ground biomass	-	+	+	-	IT	-	+	+	-	SI	-	+	+	-	IT	-	+	+	-	IT	-	+	+	+	ST
Below-ground biomass	-	+	+	-	IT	+	+	+	-	SI	+	+	+	-	SI	+	-	-	-	SI	not significant				na
Root:shoot ratio	+	+	+	-	SI	-	-	-	+	ST	+	+	+	-	SI	+	+	-	-	SI	+	-	+	+	IT
Leaf Area Ratio (LAR)	not significant				na	+	-	-	-	SI	not significant				na	not significant				na	not significant				na
Specific Leaf Area (SLA)	not significant				na	+	-	-	+	IT	+	+	-	+	IT	not significant				na	-	-	-	+	ST
Leaf Weight Ratio (LWR)	not significant				na	+	-	-	-	SI	+	-	-	-	SI	-	+	-	-	IT	not significant				na
Overall Trend	Intermediate to shade intolerant					Intermediate to shade intolerant					Intermediate to shade intolerant					Intermediate to shade intolerant					Intermediate to shade tolerant				

Responses to light intensities are summarised on the basis of absolute values as positive (+) or negative (-) responses. The light intensity treatments were: 59, 29, 17 and 6% of full sunlight. SI=shade intolerant, ST=shade tolerant, and IT=intermediate. It was not applicable (na) to assign a symptom (S) for a species if all responses were "+" or if the responses did not differ significantly within that species.

under the low light treatment with increased leaf turnover. The results suggest that, in the field, *C. australis* is likely to survive under a low-light environment, such as deep canopy shade, with increasing leaf longevity. *C. moti* had a low leaf turnover under 59% sunlight intensities. *Licuala ramsayi* did not show any clear pattern but the responses demonstrated that this species may survive both low and high light intensities.

Increased leaf turnover under high light intensities shown by some species indicated that they allocated their resources to new leaves in response to the increased light. Under more shaded treatments, when light is limited, some study species had increased leaf turnover, suggesting they tended to shed their leaves as the photosynthetic capacity was reduced. Perhaps increased leaf turnover in the palm seedlings was a response to light competition by shedding unproductive, over-shaded leaves in the lower part of the canopy (seedling crown) and replacing them with new, productive leaves in the top of the canopy. Poorter and Boot (1998) found that the leaf turnover of some rainforest tree seedlings (non-palms) increased with an increase in sunlight intensities. An experimental defoliation of the palm *Sabal palmetto,* conducted by McPherson and Williams (1998), showed that young seedlings had large resources of carbon that allowed them to survive defoliation and periods of stress.

The leaf areas of the palm seedlings studied responded differently under different light intensities (Table 2). However, the differences were not significant in *H. wendlandiana* and *L. ramsayi*. This is different to the responses found for non-palm rainforest tree species studied by Poorter and Boot (1998), *Cecropia* sp., *Schizolobium amazonicum*, *Cedrela odorata*, *Amburana cearensis*, *Astronium lecointei*, *Tetragastris altissima* and *Theobroma speciosum* had greater leaf areas with increasing light availability due to increasing competition for light during gap phase regeneration. Leaf areas of ten tropical rainforest species studied by Popma and Bongers (1988) also increased with increased light intensities.

By contrast, the leaf area of *L. ramsayi* palm seedlings were greater under lower light intensities, perhaps to maximise leaf surfaces to capture available light as shown by the increase of leaf mass and above-ground biomass. These results were in accordance with a non-palm species, *Impatiens parviflora*, which increased its leaf area with an increase in shading (Evans & Hughes, 1961).

The leaf areas of palm seedlings of *A. australasica*, *C. australis* and *C. moti* were greater under higher light intensities, except the highest. These results suggest that under 17-29% openness sunlight, they would respond to high irradiance with a greater leaf surface for maximising light capture; however, they reduced the leaf areas under 59% sunlight to inhibit water loss. Under the more shaded treatments, *A. australasica* did not allocate resources into leaf expansion, but rather into petiole and leaf blade elongation (expressed as 'height'). Similarly *C. australis* and *C. moti* did not increase leaf area under low light intensities. Therefore, *A. australasica*, *C. australis* and *C. moti* also exhibited their adaptability to a wide range of light intensities.

In addition, the responses of *C. australis* and *C. moti* to higher light intensities (although the leaf areas were lowest under the highest and lowest light intensities) suggest that in the field, under canopy gaps, they would respond to high irradiance by producing a greater leaf surface to maximize light trapping for photosynthesis; but, this study showed that these species reduced their leaf areas under 59% sunlight (equivalent to very big canopy gaps). However, the leaves of *C. australis* and *C. moti* were pinnate, so they expanded the leaf area by increasing the number of leaflets, showing the response of a species relates to its leaf morphology. This suggests that plants increase their leaf area to a maximum level, according to their leaf morphological characteristics, when further resource allocation to maximize leaf area becomes no longer efficient.

The effects of light intensity on total leaf chlorophyll content was not significant in all species, however, there were some trends in *A. australasica* (Table 2). In *A. australasica*, it was not possible to differentiate between responses under the 59, 29 and 17% light intensities; the only clear cut distinction was at the lowest light intensity, where the lowest total chlorophyll content was found. In the field, this trait, lower total chlorophyll content when light is limited, is an adaptive response to survive the low-light stress in which the photosynthesis capacity is reduced (Atwell *et al.,* 1999). The low level of resources allocated to chlorophyll content was also related to an increase in resources allocated to other traits such as leaf turnover. The results in *A. australasica* agree with the observation that somegreen plants produce more chlorophyll when the light availability increases (Atwell *et al.,* 1999). *Arenga australasica* did not allocate resources into leaf expansion under limited light where the photosynthetic capacity would be limited.

The effects of light intensity on chlorophyll *a:b* ratio were also not significant in all species. These results also suggest that chlorophyll *a:b* ratio is species dependent, as in other species, such as the non-palm species, *Alocasia macrorrhiza,* chlorophyll *a:b* ratio increased with increasing light intensities (Chow *et al.,* 1988). Most green plants contain chlorophyll *a* which generally constitutes about three-quarters of the total chlorophyll content, with the remainder accounted for by chlorophyll *b* (Raven *et al*., 1999). The chlorophyll *a:b* ratio changes with changing light intensities as the plants change their resource allocation to Photosystem I (PSI) and PSII in their photosynthesis reactions, *i.e.* different chlorophyll *a:b* ratios are involved in each Photosystem. Thus, the chlorophyll *a:b* ratio is lower under canopies where the red:far red ratio is lower; and, a higher chlorophyll *a:b* ratio occurs in canopy gaps where the red:far red ratio is higher.

Root or below-ground biomass showed no clear trend in the palm seedlings studied under different light intensities, although, there was a small change in the below-ground biomass of *L. ramsayi*. The root or below-ground biomass of *C. australis* was higher under the higher light intensities. Atwell *et al.* (1999) reported sun plants produce a high root:shoot ratio to deal with high photosynthetic capacity. The six survival traits, discussed above, maintained the vigor of some palm seedlings under different light intensities, but not all (Table 2).

Arenga australasica and *H. wendlandiana* show features which suggest that they are more adapted to survive in higher light intensities. After 34 weeks, the vigor of *A. australasica* palm seedlings was maintained at 100%, and after 67 weeks it only decreased slightly to 93% (one seedling) under the highest light intensity, indicating its adaptability to a wide range of light intensities. This suggests that *A. australasica* is likely to survive in canopy gaps. All *H. wendlandiana* seedlings showed vigorous growth after 34 weeks, however, after 67 weeks only 40% of the seedlings appeared likely to survive under 6% sunlight, suggesting this species is also likely to survive in canopy gaps in the field. *Licuala ramsayi* was able to survive in the highest and lowest light intensities for at least 34 weeks, but after 67 weeks only 40% of seedlings appeared likely to survive, suggesting it is shade tolerant (but not under 6% sunlight).

Calamus australis and *L. ramsayi* are likely to survive in higher light intensities for at least 47 and 34 weeks respectively, and then become unlikely to survive after 94 and 67 weeks respectively. This suggests, in the field, *C. australis* and *L. ramsayi* are likely to survive in canopy gaps for several months, but the results suggest that their vigor would decline over longer periods. In the current experiment, *C. australis* seedling vigor was maintained at 90-100% after 47 weeks, however, it declined considerably after 94 weeks (under 6% and 59% sunlight). As the vigor was defined by senescence, it is related to increased leaf turnover. In addition, the vigor of seedlings of *A. australasica* under different light intensities may be caused by the use of sprouted seeds rather than transplanted seedlings, which resulted in seedlings with a healthier root system.

Greater yields of leaf and above-ground biomasses were found under the higher light treatments. Higher leaf mass was found under the intermediate light intensities (29 and 17% sunlight) in *A. australasica, C. australis* and *C. moti,* reflecting the higher leaf area of these species in these treatments.

A. australasica, *C. australis* and *C. moti* had greater above-ground biomass under intermediate light intensities. Above-ground biomass was higher under the higher light intensity in *H. wendlandiana*. On the other hand, *L. ramsayi* yielded more above-ground biomass under the lower light intensities. In *H. wendlandiana*, this was consistent with the responses that this species exhibited in leaf area, leaf mass, below-ground biomass and LWR, which suggests the adaptability of *H. wendlandiana* to a wide range of light intensities.

Arenga australasica, *C. moti* and *H. wendlandiana* produced higher root:shoot ratios under higher light intensities. By contrast, *C. australis* and *L. ramsayi* tended to increase their root:shoot ratio under lower light intensities; however, the highest response was under 59% in *L. ramsayi*. It suggests that under natural conditions, *C. australis* and *L. ramsayi* would respond to higher light intensities by allocating more of their resources to roots to maximize water absorption.

In the current study, leaf area ratio (LAR) was significantly different under the higher light treatments in *C. australis*. This did not fulfill the expectation that an increase in shade intensity would cause an increase in LAR (leaf area), as suggested by Atwell *et al.* (1999). This may be caused by the responses of *Calamus* to expand their leaf areas in maximum light intensities to maximize their photosyntheses when the number of single leaflets in each their pinnate leaves was insufficient.

A decrease in leaf thickness as indicated by the increased SLA was found under the higher light treatments in all palm study species except *H. wendlandiana*. These findings agree with the observation that an increase in light intensity can lead to increased SLA or reduced leaf thickness (Atwell *et al.,* 1999). *Hydriastele wendlandiana* showed the opposite response. This may indicate a response of this species to maximize light capture for photosynthesis under low light conditions.

There was little variation in LWR with light treatments except in *H. wendlandiana.* These results were opposite to the LWR of non-palm species such as *Q. pagoda* that showed high LWR under 27 or 8% sunlight (Gardiner & Hodges, 1998). These findings suggest a greater allocation of total plant dry weight to leaves under a higher light environment in *H. wendlandiana.* This may reflect an increasing growth rate under higher light intensities.

CONCLUSION

Arenga australasica, *C. australis*, *C. moti* and *H. wendlandiana* appear suitable for revegetating large low-shade canopy gaps, while *L. ramsayi* appears best-suited for subsequent restoration where this palm species is planted subsequently to the formation of canopy. The light conditions resulting from disturbance by cyclones would favour the recruitment and seedling establishment of *A. australasica*, *C. australis*, *C. moti* and *H. wendlandiana*, while *L. ramsayi* would be favoured by intermediate levels of disturbance. Of course, this does not relate to the response of *C. australis* and *C. moti*, which are already established in the understorey at the time of disturbance.

REFERENCES

ANDERSON, J. M., CHOW, W. S. & GOODCHILD, D. J. 1988. Thylakoid membrane organisation in sun/shade acclimation. In: EVANS, J. R., VON CAEMMERER, S. & ADAMS III, W. W. (Eds.). *Ecology of Photosynthesis in Sun and Shade*. CSIRO, Melbourne. Pp. 11–26.

ATWELL, B. J., KRIEDEMANN, P. E. & TURNBULL, C. G. N. 1999. *Plants in Action: Adaptation in Nature, Performance in Cultivation*. MacMillan Publishers Australia Pty Ltd., South Yarra.

BULLOCK, J. M. 2000. Gaps and seedling colonization. In: FENNER, M. (Ed.). *Seeds: The Ecology of Regeneration in Plant Communities. 2nd edition.* CABI Publishing, Wallingford. Pp. 375–395.

CHOW, W. S., QIAN, L., GOODCHILD, D. J. & ANDERSON, J. M. 1988. Photosynthetic acclimation of *Alocasia macrorrhiza* (L.) G. Don to growth irradiance: structure, function and composition of chloroplasts. In: EVANS, J. R., VON CAEMMERER, S. & ADAMS III, W. W. (Eds.). *Ecology of Photosynthesis in Sun and Shade.* CSIRO, Melbourne, Australia. Pp. 107–122.

DOWE, J. L. 2009. A preliminary note on the impact of Cyclone Larry on Populations of *Archontophoenix alexandrae* (Arecaceae), North Queensland, Australia. *Palms and Cycads* 1: 4–8.

DRANSFIELD, J. 1979. *A Manual of the Rattans of the Malay Peninsula*. Malaysian Forest Department, Kepong.

EVANS, G. C. & HUGHES, A. P. 1961. Plant growth and the aerial environment. I. Effect of artificial shading on *Impatiens parviflora. New Phytologist* 60: 150–180.

FRANGI, J. L. & LUGO, A. E. 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. *Biotropica* 30: 339–348.

GARDINER, E. S. & HODGES, J. D. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. *Forest Ecology and Management* 108: 127–134.

GASPERSZ, V. 1991. *Research Design Methods for Agricultural, Engineering and Biological Sciences.* Indonesian translation. CV ARMICO, Bandung.

GORMAN, R. M. 1996. Demographic trends in *Licuala ramsayi* (F. Muell.) Domin (Arecaceae), Tam O'Shanter State Forest, Mission Beach, North Queensland. *Mooreana* 6: 63–78.

HENDERSON, A. 2002. *Evolution and Ecology of Palms*. The New York Botanical Garden Press, New York.

LAMBERS, H., CHAPIN III, F. S. & PONS, T. L. 1998. *Plant Physiological Ecology*. Springer-verlag, New York.

LARCHER, W. 2003. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups. Fourth edition*. Springer-Verlag, Berlin.

LATIFAH, D., CONGDON, R. A. & HOLTUM, J. A. 2014. A physiological approach to conservation of four palm species: *Arenga australasica*, *Calamus australis*, *Hydriastele wendlandiana* and *Licuala ramsayi*. *Reinwardtia* 14(1): 237–247.

MANOKARAN, N. 1985. Biological and ecological considerations pertinent to the silviculture of rattans In: WONG, K. & MANOKARAN, N. (Eds.). *Proceedings of the Rattan Seminar, 20-24 October 1984.* The Rattan Information Center, Forest Research Institute, Kepong. Pp. 95–105.

MARR, I. L., SURYANA, N., LUKULAY, P. & MARR, M. I. 1995. Determination of chlorophyll a and b by simultaneous multi-component spectrophotometry. *Fresenius Journal of Analytical Chemistry* 352: 456–460.

McPHERSON, K. & WILLIAMS, K. 1998. The role of carbohydrate reserves in the growth, resilience, and persistence of cabbage palm seedlings (*Sabal palmetto*). *Oecologia*117: 460–468.

MILES, J. & SHEVLIN, M. 2001. *Applying Regression and Correlation A Guide for Students and Researchers*. Sage Publication Ltd. New York.

POORTER, L. & BOOT, R. G. A. 1998. Seedling growth of Bolivian rainforest tree species in relation to light and water availability http://www.promab.org/lourens_poorter/contents_thesis_1p.htm. Accessed on 30 August 2008. Thesis. El Programa Manejo de Bosques de la Amazonia Boliviana (PROMAB), Riberalta.

POPMA, J. & BONGERS, F. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forests species. *Oecologia* 75: 625–632.

RAVEN, P. H., EVERT, R. F. & EICHHORN, S. E. 1999. *Biology of Plants. Sixth edition* W. H. Freeman and Company, New York.

STEEL, R. G. D. & TORRIE, J. H. 1980. *Principle and Procedure of Statistics: A Biometrical Approach.* Second Ed. McGraw Hill International Book Inc., Toronto.

TOMLINSON, P. B. 1990. *The Structural Biology of Palms*. Clarendon Press, Oxford.

TURTON, S. 2008. Cyclones Larry and Monica: ecological effects of two major disturbance events. *Austral Ecology* 33: 365–367.

WEBB, L. J. 1958. Cyclones as an ecological factor in tropical lowland rainforest, north Queensland. *Australian Journal of Botany* 6: 220–228.

INSTRUCTION TO AUTHORS

Scope. *Reinwardtia* is a scientific irregular journal on plant taxonomy, plant ecology and ethnobotany published in June and December. Manuscript intended for a publication should be written in English.

Titles. Titles should be brief, informative and followed by author's name and mailing address in one-paragraphed.

Abstract. English abstract followed by Indonesian abstract of not more than 250 words. Keywords should be given below each abstract.

Manuscript. Manuscript is original paper and represent an article which has not been published in any other journal or proceedings. The manuscript of no more than 36 pages by using Times New Roman 11, MS Word for Windows of A4 with double spacing, submitted to the editor through <reinwardtia@mail.lipi.go.id> or in our website: http://e-journal.biologi.lipi.go.id/index.php/reinwardtia/index. New paragraph should be indented in by 5 characters. For the style of presentation, authors should follow the latest issue of Reinwardtia very closely. Author(s) should send the preferred running title of the article submitted. Every manuscript will be sent to two blind reviewers.

Identification key. Taxonomic identification key should be prepared using the aligned couplet type.

Nomenclature. Strict adherence to the International Code of Botanical Nomenclature is observed, so that taxonomic and nomenclatural novelties should be clearly shown. English description for new taxon proposed should be provided and the herbaria where the type specimens area deposited should be presented. Name of taxon in taxonomic treatment should be presented in the long form that is name of taxon, author's name, year of publication, abbreviated journal or book title, volume, number and page.

Map/line drawing illustration/photograph. Map, line drawing illustration, or photograph preferably should be prepared in landscape presentation to occupy two columns. Illustration must be submitted as original art accompanying, but separated from the manuscript. The illustration should be saved in JPG or GIF format at least 350 pixels. Legends or illustration must be submitted separately at the end of the manuscript.

References. Bibliography, list of literature cited or references follow the Harvard system as the following examples.

Journal : KRAENZLIN, F. 1913. *Cyrtandraceae* novae Philippinenses I. *Philipp. J. Sci.* 8: 163–179.
MAYER, V., MOLLER, M., PERRET, M. & WEBER, A. 2003. Phylogenetic position and generic differentiation of *Epithemateae* (*Gesneriaceae*) inferred from plastid DNA sequence data. *American J. Bot.* 90: 321–329.
Proceedings : TEMU, S. T. 1995. Peranan tumbuhan dan ternak dalam upacara adat "Djoka Dju" pada suku Lio, Ende, Flores, Nusa Tenggara Timur. In: NASUTION, E. (Ed.). Prosiding Seminar dan Lokakarya Nasional Etnobotani II. LIPI & Perpustakaan Nasional: 263–268. (In Indonesian).
SIMBOLON, H. & MIRMANTO, E. 2000. Checklist of plant species in the peat swamp forests of Central Kalimantan, Indonesia. In: IWAKUMA, T. *et al*. (Eds.) Proceedings of the International Symposium on: Tropical Peatlands. Pp.179-190.
Book : RIDLEY, H. N. 1923. *Flora of the Malay Peninsula 2*. L. Reeve & Co. Ltd, London.
Part of Book : BENTHAM, G. 1876. *Gesneriaceae*. In: BENTHAM, G. & HOOKER, J. D. *Genera plantarum 2*. Lovell Reeve & Co., London. Pp. 990–1025.
Thesis : BAIRD, L. 2002. *A Grammar of Kéo: An Austronesian language of East Nusantara*. Australian National University, Canberra. [PhD. Thesis].
Website : http://www.nationaalherbarium.nl/fmcollectors/k/KostermansAJGH.htm). Accessed 15 February 2012.

Reinwardtia
Published by Herbarium Bogoriense, Botany Division, Research Center for Biology,
Indonesian Institute of Sciences
Address: Jln. Raya Jakarta-Bogor Km. 46 Cibinong 16911, P.O. Box 25 Cibinong
Telp. (+ 62) 21 8765066; Fax (+62) 21 8765062
E-mail: reinwardtia@mail.lipi.go.id

REINWARDTIA Author Agreement Form

Title of article :

Name of Author(s) :

I/We hereby declare that:

- My/Our manuscript was based on my/our original work.
- It was not published or submitted to other journal for publication.
- I/we agree to publish my/our manuscript and the copyright of this article is owned by Reinwardtia.
- We have obtained written permission from copyright owners for any excerpts from copyrighted works that are included and have credited the sources in our article.

Author signature (s) Date

Name

REINWARDTIA
Vol. 15. No. 2. 2016

CONTENTS

Page

Reinwardtia is a LIPI accredited Journal (792/AU3/P2MI-LIPI/04/2016)
http://e-journal.biologi.lipi.go.id/index.php/reinwardtia

Herbarium Bogoriense
Botany Division
Research Center for Biology – Indonesian Institute of Sciences
Cibinong Science Center
Jln. Raya Jakarta − Bogor, Km 46
Cibinong 16911, P.O. Box 25 Cibinong
Indonesia