Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in response to light acclimation — Source link

Philippe Saner, Christopher D. Philipson, Shaun Peters, Felix Keller ...+3 more authors

Institutions: University of Zurich, ETH Zurich, Stellenbosch University, University of Oxford

Related papers:

- Different light acclimation strategies of two coexisting tree species seedlings in a temperate secondary forest along five natural light levels

- Carbohydrate storage, survival, and growth of two evergreen Nothofagus species in two contrasting light environments

- Acclimation to a Change in Light Regime in Seedlings of Six Australian Rainforest Tree Species

- The effect of low irradiance on growth,photosynthetic characteristics,and biomass allocation in two deciduous broad-leaved tree seedlings in southeast of Hubei Province

- Photosynthesis in relation to growth and seedling ecology of two dipterocarp rain forest tree species

Year: 2016

Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in response to light acclimation

Saner, Philippe ; Philipson, Christopher D ; Peters, Shaun ; Keller, Felix ; Bigler, Laurent ; Turnbull, Lindsay A ; Hector, Andy

Abstract: Background: Acclimation to light is a driver of tropical forest dynamics and key to understanding the coexistence of dipterocarps, and how their demographic rates and traits trade-off. Aims: We examined light niche divergence in six dipterocarp species and hypothesised that seedlings can be functionally grouped, and allocate resources to either growth or storage in response to light changes. Methods: A pot experiment was performed to measure size-specific growth rate, wood density and total non-structural carbohydrate (NSC) concentrations of dipterocarp seedlings exposed to a simulated gap opening. Results: Light-demanding species responded to a gap opening with increased growth and decreased wood density, whereas shade-tolerant species showed a greater relative increase in NSC concentration. Iditol – an alditol – was identified, and Dryobalanops lanceolata responded to a gap opening with a significantly smaller increase in alditol concentration compared to other species. Conclusions: We group light-demanding and shade-tolerant species based on their acclimation to light and show that a generalist species is unique based on its response of NSC concentration to a gap opening. Our findings emphasise that the ecology of these species needs to be further studied in the context of their physiology to support their effective use in large-scale forest restoration efforts.

1   **Title**

2   Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in

3   response to light acclimation

4

5   **Authors**

6   Philippe Saner [1], Christopher D. Philipson [2], Shaun Peters [3], Felix Keller [4], Laurent Bigler[5], Lindsay

7   A. Turnbull [6], Andy Hector [6]

8

9   **Corresponding author**

10   Philippe Saner*, email: philippe.saner@uzh.ch, tel: +41 44 635 5487, fax: +41 44 635 5711

11

12   [1] Institute of Evolutionary Biology and Environmental Studies, University of Zürich,

13   Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

14   [2] Ecosystem Management, Institute of Terrestrial Ecosystems, ETH Zürich, Universitätsstrasse 16,

15   CH-8092 Zürich, Switzerland. Email: christopher.philipson@usys.ethz.ch, phone: +41 44 632 68

16   05

17   [3] Institute for Plant Biotechnology, Department of Genetics, Faculty of AgriSciences, Stellenbosch

18   University, Matieland 7602, Stellenbosch, South Africa. Email: swpeters@sun.ac.za, phone: +27

19   021 808 9372

20   [4] Institute of Plant Biology, Molecular Plant Physiology Division, University of Zürich,

21   Zollikerstrasse 107, CH-8008 Zürich, Switzerland. Email: fkel@botinst.uzh.ch, phone: +41 44 634

22   82 82

23   [5] Department of Chemistry, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich,

24   Switzerland. Email: laurent.bigler@chem.uzh.ch, phone: +41 44 635 42 86

1   [6] Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, OX1 3RB, UK.

2   Email: lindsay.turnbull@plants.ox.ac.uk, phone: +44 1865 275145. Email:

3   andrew.hector@plants.ox.ac.uk, phone: +44 1865 275032

4

10

Disclosure Statement

12   The authors declare that they have no conflicts of interest. The authors acknowledge that they have

13   no financial interest or benefit arising from the direct applications of this research.

14

Notes on Contributors

16   **Philippe Saner** is an environmental scientist with a main interest in tropical plant community

17   ecology and the restoration of tropical forests.

18   **Christopher D. Philipson** is a quantitative ecologist interested by the diversity of natural

19   ecosystems and understanding the processes that maintain diversity.

20   **Shaun Peters** is a lecturer with a research interest within the broad purvey of plant water-soluble

21   carbohydrate metabolism.

22   **Felix Keller** is a professor emeritus with a research interest in water-soluble carbohydrates in

23   plants.

24   **Laurent Bigler** is head of the mass spectrometry lab with a strong interest in the identification of

25   new compounds associated with plant metabolism.

1 **Lindsay A. Turnbull** is an associate professor with a research interest in how and why plant

2 species are so different to each other, and what the consequences of these differences may be for

3 ecosystems.

4 **Andy Hector** is a community ecologist interested in biodiversity loss and its consequences for the

5 stability and functioning of ecosystems and the provision of ecological services.

6

7 **Figures:** 5

8 **Tables:** 1

9 **Electronic supplementary material:** 1 figure

1   **Abstract**

2   **Background:** Acclimation to light is a driver of tropical forest dynamics and key to understanding

3   the coexistence of dipterocarps, and how their demographic rates and traits trade-off.

4   **Aims:** We examined light niche divergence in six dipterocarp species and hypothesised that

5   seedlings can be functionally grouped, and allocate resources to either growth or storage in response

6   to light changes.

7   **Methods:** A pot experiment was performed to measure size-specific growth rate, wood density and

8   total non-structural carbohydrate (NSC) concentrations of dipterocarp seedlings exposed to a

9   simulated gap opening.

10   **Results:** Light demanding species responded to a gap opening with increased growth and decreased

11   wood density, whereas shade-tolerant species showed a greater relative increase in NSC

12   concentration. Iditol–an alditol–was identified, and *Dryobalanops lanceolata* responded to a gap

13   opening with a significantly smaller increase in alditol concentration compared to other species.

14   **Conclusions:** We group light demanding and shade-tolerant species based on their acclimation to

15   light and show that a generalist species is unique based on its response of NSC concentration to a

16   gap opening. Our findings emphasize that the ecology of these species needs to be further studied in

17   the context of their physiology to support their effective use in large-scale forest restoration efforts.

18

1 **Introduction**

2 The ecology of tropical tree species has been studied extensively at the seedling stage and in

3 response to light, a main driver of tropical forest dynamics (Augspurger 1984; Bloor 2003; Baltzer

4 & Thomas 2007; Baraloto & Forget 2007; Philipson et al. 2012; Paine et al. 2015). Some studies

5 have tested how seedlings respond to changes in light availability that occur during sudden gap

6 formation or closure caused by tree- or branchfalls in a natural forest (Osunkoya and Ash 1991;

7 Parsons et al. 1994; Huante and Rincon 1998; Dalling et al. 2004; Philipson et al. 2014). Such

8 events dramatically alter both light availability and microclimatic conditions and offer a potential

9 regeneration niche axis along which species may be differentiated (Canham 1989; Denslow et al.

10 1998; Poorter 2005; Marthews et al. 2008). Early theoretical concepts on the importance of canopy

11 gap dynamic processes and how they drive the coexistence of tree species, such as the gap size-

12 niche partitioning (Connell 1978; Hartshorn 1978; Denslow 1980) or cross-over point irradiance

13 (Givnish 1988; Latham 1992; Sack and Grubb 2001), have been challenged for their over-simplicity

14 (Brokaw and Scheiner 1989; Raich and Christensen 1989; Brown and Whitmore 1992; Barker et al.

15 1997; Agyeman et al. 1999; Brown et al. 1999; Kitajima and Bolker 2003; Baraloto et al. 2005).

16 Mean growth rate may be positively correlated between low-light and high-light conditions and thus

17 show no rank reversal in performance among species, however comparison of mean growth rate and

18 survival for the same species may still reveal a trade-off.

19 These initial ideas of driving mechanisms that promote species diversity have been further

20 explored by expanding the spatial and temporal limits. One example is the observed trade-off in

21 seedlings to grow rapidly under high-light environments of large canopy gaps, versus the ability to

22 survive in low-light conditions typical of the forest understory (Hubbell and Foster 1992; Kitajima

23 1994; Kobe et al. 1995; Poorter 1999). In addition, the idea of ontogenetic niche shifts and the

24 divergence in regeneration niches were framed to explain how acclimation to light (light niche

25 divergence) may promote coexistence by allowing species to partition forest light conditions

26 (Myers and Kitajima 2007; Poorter and Kitajima 2007; Kitajima and Poorter 2008). For example,

1 sudden increases or decreases in light may force a seedling to selectively allocate resources into

2 structural tissue for current growth (e.g. diameter) to outcompete others for access to light or, invest

3 into denser wood or non-structural carbohydrate (NSC) storage to prolong survival (Kobe 1997;

4 Canham et al. 1999; Poorter et al. 2010). Although similar questions on light niche divergence have

5 been tackled before, this study contributes to the comparative body of literature by adding results

6 from a pot experiment with dipterocarp seedlings where we experimentally simulated a gap opening

7 event to study the effect on seedling ecophysiology with seedlings that are widely used in large-

8 scale forest restoration efforts (Hector et al. 2011).

9   The members of the *Dipterocarpaceae* (dipterocarps) family (Wyatt-Smith 1995) contribute

10 about 50% of the upper canopy trees in undisturbed lowland mixed dipterocarp forests and

11 comprise the majority of commercial timber extracted from South East Asia (Symington 1943;

12 Ashton 1982). Dipterocarps offer an ideal study system to test these proposed trade-offs between

13 investing into growth or storage. They belong to the shade-tolerant climax species, but within this

14 general category have species-specific differences based on their wood density and acclimation to

15 light (Gustafsson et al. 2016). Philipson et al. (2012) assessed trade-offs in growth rates of

16 dipterocarp seedlings and observed substantial crossovers among 21 species and no consistent

17 growth hierarchy across light treatments. This may indicate that the heterogeneity of the light

18 environment is a driving force to promote diversity in dipterocarps. Further, they assessed trade-offs

19 between mean growth rate and survival with a cross-comparison among 15 species–covering five

20 out of the six species in the present study–where the relationship in basal diameter growth and

21 probability of mortality was found to be positive (Philipson et al. 2014). In addition, this recent

22 study reported a negative relationship between wood density and the probability of mortality,

23 suggesting that wood density can serve as a surrogate for survival in the dipterocarp seedlings of

24 this study.

25   Apart from the trade-off in structural tissue (growth and wood density) an additional key

26 trait that received attention lately is NSC. Recent findings on eight dipterocarp seedlings–including

four of the species of this study–show that NSC can be linked to increased survival under simulated

drought conditions (O'Brien et al. 2014, 2015). Further, soluble sugar concentration, but not starch

concentration, was reported to significantly increase in woody tissue and decrease in leaf tissue of

Shorea beccariana and *S. parvifolia* seedlings in response to a simulated drought over 20 days

(Valtat 2015). This shows that carbohydrates may fulfill diverse roles during plant metabolic

adaptation to increased stress and mortality (McDowell and Sevanto, 2010). To what level NSC are

involved in whole plant acclimation to light is currently unknown for dipterocarps and so is the role

of water-soluble carbohydrates (WSC), and specifically alditols. Proposed ecophysiological

functions of alditols in plants are manifold and include primary products of photosynthetic carbon

assimilation, translocation and storage of carbon, and abiotic stress protection (e.g. as compatible

solutes, osmoregulators, and antioxidants) (Bieleski, 1982; Loescher & Everard, 2000). As primary

photosynthetic products, alditols may be stored in source leaves and/or exported to sink tissues

where they may also be stored and/or used for growth. Their storage function is illustrated by the

fact that alditols may easily accumulate to 10-20% of a tissue's dry weight (Dietz & Keller, 1997;

Loescher & Everard, 2000).

Hence, the motivation of this study is to elaborate on these latest findings on trade-offs

within, and between, key functional traits in dipterocarps, by forcing seedlings into an altered

carbon balance in a pot experiment to study light niche divergence. We experimentally test for

species-specific light acclimation strategies in the relative change of carbohydrates to structural

tissue to support growth or wood density versus the proportional change in total NSC concentration

or alditol concentration. Our initial hypothesis is that relative changes in selected life history

attributes in response to light acclimation allow for grouping dipterocarps into light demanders and

shade-tolerants, including a generalist species. Based on previous findings in the literature, we

predict that shade-tolerants and the generalist species will show a relative change in carbohydrates

towards denser wood –a trait that positively correlates with survival– whereas light demanders will

increase their mean relative growth. Further, we expect that shade-tolerant species and the

1 generalist, as a direct response to light acclimation, will show a greater proportional change in

2 carbohydrate concentration, whereease light demanding species will increase their mean relative

3 growth.

4

5 **Materials and methods**

6 *Experimental set-up*

7 The study site (05º05'20'' N, 117º38'32'' E, 102 m.a.s.l.) was located in the Malua Forest Reserve

8 in the eastern part of Sabah in Malaysian northern Borneo. Six climax dipterocarp species native to

9 Sabah and widely used for forest rehabilitation (Sabah Forestry Department 2008) were selected for

10 this pot experiment based on their known range in wood density (Newman et al. 1998) and differing

11 response in light acclimation (Moad 1992; Zipperlen 1997; Clearwater et al. 1999): *Dryobalanops*

12 *lanceolata, Hopea nervosa, Shorea argentifolia, Shorea leprosula, Shorea macroptera* and *Shorea*

13 *parvifolia*. Four of them are classified as endangered (*D. lanceolata, S. argentifolia* and *S.*

14 *leprosula*) or critically endangered (*H. nervosa*) according to the IUCN Red List (2015) and it is

15 therefore essential to better understand their ecology.

16

17 *Study design*

18 The experimental design consisted of ten shade houses (4 x 6 x 5 m) that were aligned in five

19 blocks of two, randomly allocated to high or low light conditions. In order to minimize self shading,

20 blocks were sited along an east-west line with 3 m space between the houses and >10 m between

21 blocks, shade houses were covered with layers of 70% black shade cloth on all sides. Within shade

22 houses, seedlings were spaced 0.3 m apart. To reduce the effect of herbivory, pots were located 0.3

23 m above ground and surrounded by wire mesh to protect seedlings from mammal damage. Light

24 conditions were simulated by using either a single or triple layer of 70% black shade cloth to mimic

25 respectively (mean ± SEM): a large gap (high; $32.9 \pm 4.5\%$ full sunlight; 127.5 ± 13.2 μmol m^{-2} s^{-1}),

26 and the forest understory (low; $2.6 \pm 0.6\%$ full sunlight; 11.7 ± 2.3 μmol m^{-2} s^{-1}) (see Saner et al.

1   2011 for a detailed description on the measurement of experimental light conditions). Light

2   conditions were representative of the surrounding logged forest and slightly higher compared to

3   previous studies as the shade cloth had worn somewhat since the shade houses were initially

4   constructed in 2005 (Saner et al. 2011; Philipson et al. 2014; see Muff et al. 2014 for a

5   comprehensive analysis of the difference between observed light values and the target values within

6   replicates).

7   All seedlings were grown from the seeds of wild fruiting trees and propagated under nursery

8   conditions ($\approx$11% full sunlight) at the study site. To minimize intraspecific variation in initial size

9   we chose seedlings of the same age (18 months) and a similar height of approximately 0.5 m.

10   Seedlings were transplanted into individual pots (0.3 x 0.4 m) using topsoil that was shredded to

11   small pieces with a rotating conveyer belt (Royer Model 110, USA) to discharge stones and woody

12   debris. In order to prevent roots from being damaged, seedlings were kept in the original soil while

13   transplanting. Seedlings were watered twice daily (morning and late afternoon) to avoid drought

14   stress and fertilized twice during the course of the experiment with 2.5 g Agroblen (Scotts PBG

15   Malaysia Sdn. Bhd., Selangor, Malaysia) 6-month slow release fertilizer (16:8:9:3, N:P:K:Mg +

16   trace elements). They were randomly relocated every month within each shade house to avoid

17   positioning effects. Four individuals of each of the six species in every shadehouse (n=240) were

18   present at the start of the experiment in August 2006. On day 155, all seedlings in the low and high

19   light shade houses were briefly moved into sunlit conditions. One individual per species from each

20   shade house was then returned to the same light level, while the other was assigned to a new shade

21   house with a different light level. This meant that half the seedlings experienced constant light

22   conditions, either low or high for the entire experimental period, while the other half spent the first

23   155 days in either low or high light and the remaining 165 days in the opposite light treatment while

24   controlling for the effect of movement between light treatments. Stem diameter (10 cm above

25   ground) was measured at day 0, 98, 155 and 320 of the experiment (Figure 1). At day 320, all

26   seedlings were harvested and green volume was measured to calculate wood density for each

1   individual plant by taking a wood sample from the lower stem following the water displacement

2   method described in Chave (2005). Samples were then oven-dried at 60°C for one week until

3   constant mass (note that this likely reduced total NSC levels by oven drying).

4

5   *Seedling growth*

6   Seedling growth rate analysis was done with the *nlme* package (Pinheiro and Bates 2000) in R 3.2.0

7   (R Development Core Team 2015). In order to estimate a seedling growth rate for each species that

8   is unbiased by differences in initial size across species, we estimated size-specific diameter growth

9   rates (SGR) (Nicieza and Alvarez 2009; Paine et al. 2012a). The growth rate was calculated by

10   fitting a non-linear power law of diameter against time for each individual seedling, for details on

11   the method see also Philipson et al. (2012, 2014). The growth rate was calculated for an average

12   diameter (5.8 mm) across all species half-way through the experiment.

13   Model convergence to estimate SGR could only be achieved for seedlings grown in constant

14   light conditions (low or high light) and which survived to the final harvest (79 individuals in total

15   across species). Non-linear models are more difficult to fit than linear models, and in this case

16   problems were compounded because some individuals simply did not grow in low light (Figure 1).

17   To overcome this problem, a small number of seedlings (n = 11) from the low light condition were

18   removed prior to analysis, in particular, *S. parvifolia* was removed completely.

19   Power laws can also be difficult to fit because of trade-offs among the three parameters: the

20   scaling exponent (α), the growth coefficient (β), and the initial diameter (M_0). We therefore decided

21   to restrict β to a single shared value among all species, which enabled us to fit individual growth

22   curves to all seedlings where predictions matched the raw data for constant light environments. The

23   selected model to estimate SGR included main effects of species ($F_{5,146} = 3.6$, $p < 0.01$) and light

24   (treated as continuous) ($F_{1,146} = 297.2$, $p < 0.0001$). The interaction was not significant and was

25   therefore not considered for calculating individual SGR. The best value of the growth coefficient β

26   was 0.1, indicating that the growth was almost linear (0 = linear; 1 = exponential).

1

NSC and WSC analyses

Analysis of NSC concentration was only carried out on seedlings growing under two light

conditions (high-light and low-light). Stem tissue from dipterocarp seedlings was shown to have

slightly higher concentrations of NSC compared to the roots or leaves (O'Brien et al. 2014), and

wood samples from the lower stem were used for carbohydrate analysis in the present study.

However, as the NSC extraction protocol of O'Brien et al. (2014, 2015) was different than in this

study a direct comparison of the NSC and WSC concentration may not be feasible (Quentin et al.

2015). Samples were collected at the final harvest (day 320), transported to the laboratory on the

day of collection and oven-dried at 60°C for one week until constant mass. Samples of >1 g dry

mass were ground to fine powder in a ball mill (Tissue-Lyser, Qiagen, Germany).

Extraction of WSC

WSC were extracted twice in 1 ml of 80% and 20% ethanol (v/v), respectively, and twice in 1 ml

deionized water (dH$_2$O) (Peters et al. 2007). For each extraction, samples were heated at 80°C for

10 min, placed on ice for 2 min, and centrifuged (15,000 g, 5 min). The supernatants of all

extraction steps were pooled and adjusted to 6 ml with dH$_2$O. WSC (sucrose, glucose, fructose,

myo-inositol and alditols) were then separated, identified and quantified by HPLC-PAD (Peters and

Keller 2009). The remaining tissue was dried at 55°C to remove residual ethanol and subsequently

used to quantify starch. Representative WSC samples were tested for lipophilic substances using a

methanol-activated reverse-phase cartridge (C$_{18}$ Sep-Pak classic: Waters, Rupperswil, Switzerland).

The HPLC chromatograms of non-delipidated and delipidated extracts were identical (data not

shown), therefore we concluded that delipidation was unnecessary.

Separation and quantification of WSC

1   Aliquots (50 µl) of WSC ethanol extracts were desalted and analyzed by HPLC-PAD (Peters &

2   Keller 2009). A Ca/Na-moderated ion partitioning carbohydrate column was used to separate WSC

3   (Benson BC-100 column; Benson Polymeric, Reno, NV, USA). It was operated at 90°C and

4   isocratically eluted with 0.005% (w/v) Ca/Na$_2$ – EDTA at a flow rate of 0.6 ml min^{-1}. The BC-100

5   chromatographic system consisted of a Gynkotek model 480 High Precision Pump, a Gynkotek

6   Gina 50 autosampler and a Jones column temperature controller (Ercatech, Berne, Switzerland).

7   WSC were detected after post-column addition of NaOH (300 mM, 0.6 ml min^{-1}) using an ESA

8   Coulochem II electrochemical detector (ESA, Cambridge, MA, USA), operated with an ESA 5040

9   analytical cell. WSC (sucrose, glucose, fructose, *myo*-inositol and alditols) were quantified against a

10   series of 5 nmol standard carbohydrates (Sigma Aldrich®, Switzerland). The quantity of standard

11   carbohydrates used corresponded to the linear response range of the chromatographic system. An

12   unknown alditol (retention time: 19.1 min) was compared to a series of 5 nmol standard alditols

13   (arabitol, erythritol, threitol, xylitol, mannitol, sorbitol, dulcitol and iditol) (supplementary material

14   Figure S1). However, the latter four hexitols showed similar retention times (around 19 min), and

15   the unknown alditol was thus further analyzed by GC/MS.

16

17   *Derivatization of alditol*

18   For derivatization of the alditol, the desalted and lyophilized samples (20 µl) were dissolved in a

19   mixture of 40 µl pyridine and 10 µl trimethylsilyl imidazole. The solution was then heated to 60˚C

20   for 30 min and 1 µl injected into a Thermo Fisher Scientific gas chromatograph-mass spectrometer

21   (GC/MS) instrument consisting of a Trace GC and a single stage quadrupole MS model DSQ. The

22   split injector was at 250˚C. The GC capillary column was DB5MS (J&W Scientific, Folsom, CA,

23   U.S.A.) and was operated from 60 to 300˚C at a gradient of 8°C min^{-1}. Helium was used as carrier

24   gas. The transfer line was at 250˚C. Mass spectra were recorded under electron impact at 70 eV,

25   over the range 74 to 322 m/z (mass-to-charge ratio) at one scan per second for the full scan mode.

26   The chromatographic peaks were identified by injection of pure compounds. Iditol was identified

1   following Rivier (2003), where the relative intensity ≥ 50% of the base peak has an absolute

2   tolerance of ± 10%, and for the range between < 50% and ≥ 25% the relative tolerance is ± 15% .

3   Two fractions (217 and 319.1) with the highest m/z could only be assigned to the iditol standard for

4   eight random samples, confirming that the alditol is indeed iditol (data not shown).

5

6   *Quantification of starch*

7   The Enzytec starch kit for food analysis was used to quantify starch (R-Biopharm, Germany).

8   Pellets were resuspended in 5 ml double distilled water and starch was gelatinized at 110°C for 30

9   min. Then aliquots (20 μl) were mixed with 20 μl AGS containing α-amyloglucosidase and α-

10   amylase and incubated at 60°C for 30 min. Aliquots (120 μl) of dH_2O were added and the

11   remaining plant debris removed by centrifugation (15,000 g, 10 min). The supernatant (120 μl) was

12   transferred into the wells (total volume 323 μl) of a microtiter plate (Greiner clear, Huber & Co

13   AG, Switzerland) and mixed with 80 μl of solution #1 (containing $NADP^+$) for the blank

14   measurement. The enzymatic reaction was initiated with 1.5 μl of solution #2 (containing

15   hexokinase and glucose-6-phosphate dehydrogenase). Absorbance was measured after 6 min, at 2

16   min intervals (reaction peak 14 min) at a wavelength of 340 nm. A glucose (Fluka[®], Switzerland)

17   standard was used for starch quantification; starch is expressed as $glucose_{eq}$ (McCready et al. 1950).

18   Quantification was performed on a Spectra Max M2 plate reader (Bucher Biotec, Switzerland)

19   using the SoftMax Pro 4.7.1 (Molecular Devices, Sunnyvale, CA, USA).

20

21   *Statistical analysis*

22   In a first step, as already described above in detail, the individual seedling SGR was calculated with

23   a linear mixed-effects model. In a second step, individual seedling SGR, wood density and NSC

24   concentration (including starch, WSC and iditol) were then treated as dependent variables in a

25   second linear mixed-effects model and tested against species, functional group and light treatment

26   (fixed effects). Shade house (n=5) and individual shade houses (n=10) were treated as random

1 effects. Where needed, heteroscedasticity was controlled for by modelling increasing variance with

2 the varPower function, or in the case of total NSC concentration, starch and iditol concentration the

3 dependent variable was simply log-e transformed. In a third step, Pearson's product moment

4 correlation was used to test for correlations between species mean values of SGR, wood density,

5 NSC concentration and iditol concentration. NSC concentration (%), but not pool size (total mg),

6 was included in the analyses.

7

8 **Results**

9 *Growth and wood density*

10 A significant main effect of wood density ($F_{1,35} = 121.4$, $p<0.0001$), light condition ($F_{1,4} = 164.0$,

11 $p=0.0002$) and functional group ($F_{1,35} = 9.8$, $p=0.0035$) on diameter SGR was observed, however

12 neither two-way interactions between wood density, light condition and functional group nor the

13 three-way interaction were found to be significant (Figure 2). The negative correlation between

14 mean diameter SGR and mean wood density across all six species was stronger in high light

15 ($r=0.92$, $t=4.6$, $df=4$, $p=0.01$, 95% CI: 0.99 to -0.41) compared to low light ($r=0.85$, $t=2.9$, $df=3$,

16 $p=0.06$, 95% CI: -0.99 to 0.11) (Figure 2). Overall, an increase in light decreased wood density by

17 0.07 g cm^{-3} ($F_{1,4} = 11.7$, $p<0.05$, average wood density in low-light: 0.69 g cm^{-3}, high-light: 0.62 g

18 cm^{-3}). A light increase resulted in a marginally ($F_{1,48} = 3.6$, $p=0.06$) higher shift in wood density in

19 light demanders (0.13 g cm^{-3} relative change (20%): average in low light: 0.65 g cm^{-3}, average in

20 high light: 0.52 g cm^{-3}) compared to shade tolerants (0.04 g cm^{-3} relative change (5%): average in

21 low light: 0.73 g cm^{-3}, average in high light: 0.69 g cm^{-3}).

22 A positive correlation ($r = 0.96$, $t = 6.3$, $df = 3$, $p < 0.01$, 95% CI: 0.55 to 1.00) was found

23 between species mean SGR in high-light and mean SGR in low-light conditions. Overall, the light

24 demanders *S. argentifolia* and *S. leprosula* had a faster diameter growth rate compared to the shade-

25 tolerants *H. nervosa* and *S. macroptera* or the generalist *D. lanceolata* (Figure 3).

26

14

1   *Relative change in NSC concentration and light acclimation*

2   Seedlings of all six species showed lower total NSC concentrations ($F_{1,4} = 60.9$, $p < 0.01$) in low-

3   light compared to the high-light condition and adjusted total NSC concentration within five months

4   of translocation (Figures 4a and d). Acclimation to a sudden light increase (gap opening) resulted in

5   a significantly different proportional increase in total NSC concentration across species ($F_{5,20} = 3.2$,

6    $p < 0.05$). Overall the shade-tolerants (including the generalist species) showed a greater relative

7   increase in NSC concentration compared to light demanders as a direct response to a simulated gap

8   opening ($F_{1,24} = 5.7$, $p < 0.05$). NSC was further separated and analysed based on components,

9   however the finding was consistent with total NSC concentrations when testing for starch

10   concentration ($F_{1,24} = 4.7$, $p < 0.05$) or WSC concentration ($F_{1,24} = 4.0$, $p = 0.06$).

11

12   *Growth and storage*

13   The relationship between the proportional increase in total NSC concentration after a gap opening

14   (Δ NSC between low and low-high condition) and the average species growth rate under the high-

15   light condition was further examined across species and functional group (Figure 5). Overall, we

16   found no significant relationship between growth and storage across species. In particular, the

17   generalist *D. lanceolata* responded with a slower growth rate and a proportionally lower relative

18   increase in total NSC concentration as a response to a gap opening. Once this species was excluded,

19   the relationship between the relative change in growth or storage was significant for the remaining

20   five species ($r = 0.96$, $t = 5.6$, $df = 3$, $p = 0.01$, 95% CI: -0.99 to -0.47). However, the light

21   demanders *S. argentifolia, S. leprosula* and *S. parvifolia* invested only marginally less to NSC

22   concentration compared to the shade-tolerants *H. nervosa* and *S. macropera* ($F_{1,3} = 7.6$, $p = 0.07$).

23

24   *Contribution of alditols to total NSC concentration*

25   WSC contributed 42–87% to total NSC concentration, depending on species and light condition

26   (Table 1). A main compontent of WSC was identified as iditol, an alditol present in all six species

1   and under all light conditions with a relative concentration compared to total NSC that ranged

2   between 3-47% (mean absolute concentration: 0.1-17.8 mg g^{-1}) (Table 1). Despite the overall

3   difference in iditol concentration between low light compared to high light conditions, the

4   interaction between treatment and species indicated that the increase was not signifcant for all

5   species ($F_{5,40}$ = 2.4, p = 0.05) (Figure 4b and c). However, seedlings across all six species adjusted

6   iditol concentrations within five months to their present light condition, suggesting that the trait is

7   highly adaptive (Figure 4a and d). Seedlings that were translocated from high to low light showed a

8   significantly lower proportional increase in iditol concentrations than seedlings that were constantly

9   exposed to low light ($F_{1,4}$ = 29.5, p < 0.01). Interestingly, the generalist *D. lanceolata* showed a

10   significantly smaller increase in iditol concentration as a direct response to a gap opening compared

11   to all other species ($F_{1,24}$ = 15.8, p < 0.0001). Correlation between iditol concentration and other

12   traits did not reveal any significant patterns across species and an inconsistent pattern was observed

13   within species where a negative relationship between the relative increase in iditol concentration

14   and wood density in the high light condition was found for three of the six dipterocarp species (*S.*

15   *macroptera, S. argentifolia, S. leprosula*).

16

17   **Discussion**

18   Clearly, the selection of species and the replication within each functional group is not

19   representative to study light niche divergence across the full ecological range with more than 250

20   species of dipterocarps for Borneo alone (Ashton 2004). However, based on the contrast analysis

21   performed between functional group in response to light acclimation we can group the six

22   dipterocarp species based on their changes in selected life history attributes into a light demanding

23   group including *S. argentifolia, S. leprosula* and *S. parvifolia*; and a shade-tolerant group including

24   *Hopea nervosa*, *S. macroptera* and the generalist *D. lanceolata*. Overall, light demanding species

25   responded to a gap opening with increased growth and a greater relative decrease in wood density,

26   whereas shade-tolerant species showed a greater relative increase in NSC concentration.

1   Investing into growth may be the single most important strategy for dipterocarps to escape

2   the light limited environment of a tropical forest understory after a sudden gap opening (Gustafsson

3   et al. 2016). However, in contrast to the findings of Philipson et al. (2012), who reported substantial

4   crossovers among 21 species and no consistent growth hierarchy across light treatments, in the

5   present study we found no crossovers in growth rates across light conditions and light demanders

6   showed proportionally higher growth compared to shade-tolerants or the generalist species. Wright

7   et al. (2010) and Kitajima and Bolker (2003) emphasized that seedlings that grow well in high light

8   also show higher mortality and reduced stability and resistance in the dark. In dipterocarps, this

9   mechanism was reported recently, where the relationship in basal diameter growth and expected

10   probability of mortality was found to be positive, and probability of mortality also correlated

11   negatively with wood density (Philipson et al. 2014). Testing for a growth-mortality trade-off

12   requires a negative carbon balance or at least reduced growth in the shade as compared to light

13   conditions (Myers and Kitajima 2007). During our experiment, none of the seedlings in the

14   experimental treatment died and although NSC concentration was low it was not fully depleted

15   even in low-light conditions and with little growth over ten months. For example, *S. parvifolia*

16   seedlings did not grow in low light (Figure 3), although NSC concentration for this species was

17   comparable to other species (Table 1 and Figure 4c). This reflects the ecology of dipterocarp

18   seedlings, which are well known to be able to persist in the dark forest understorey close to their

19   light compensation point for years (Watling et al. 1997; Eschenbach et al. 1998; Leakey et al.

20   2003). The relative change towards increased wood density across all species as a response to low-

21   light conditions was minimal on average, but resulted in a relative change of 20% in light

22   demanding species which could suggest that wood density may be related to avoidance of structural

23   damage for prolonged survival, as has been proposed for bark thickness in response to fire regimes

24   at the global scale (Pausas 2015). However, the functional role of a high wood density is yet unclear

25   and a global assessment indicated only a weak negative relationship between wood density and

1   sapling growth (Larjavaara and Muller-Landau 2012; Philipson et al. 2014; but see Paine et al.

2   2015).

3   As dipterocarps are well known to be resistant to averse environmental conditions the

4   proportional change in storage may support their prolonged survival under drought (O'Brien et al.

5   2014) and under light acclimation. By examining the proportional change in NSC and alditol

6   concentrations, we include additional non-structural traits that have been proposed to be related to

7   the life history strategies of tropical tree seedlings (Kobe 1997; Myers and Kitajima 2007; Poorter

8   and Kitajima 2007; Poorter et al. 2010). Our results indicate that seedlings of selected dipterocarps

9   respond to a sudden light increase with differing strategies and that the increase in NSC

10   concentration is perhaps not only a reaction to resource limitation. Whereas light demanding

11   species show a greater increase in growth to outcompete others in the race for canopy access, we

12   found that they increase proportionally less in storage. We therefore argue that the exposure to

13   sudden light changes and subsequent changes in storage levels,-such as the response to a gap

14   opening as described above, is a successful experimental approach to indicate life-history strategies

15   and associated trade-offs in key functional traits. It is important to note that the findings presented

16   here are based on a pot experiment, where seedlings in the constant high light environment showed

17   signs of being pot bound with modified roots (roots moving around the walls of the pot in a circular

18   fashion). We can therefore not conclude that the results are directly comparable to what happens in

19   the field under more natural conditions.

20   Still, little is known about the functional role of NSC and its sub-components (starch and

21   soluble sugars) in dipterocarps. The results presented here are based on lower stem tissue only and

22   do not include root or leaf NSC concentration. Dipterocarp seedlings of the species presented here

23   were shown to have slightly higher but comparable concentrations of NSC in stem compared to

24   roots or leaves (O'Brien et al. 2014, but see Quentin et al. 2015). Carbohydrate concentration in

25   dipterocarps was found to increase during drought periods and especially soluble sugars could be

26   important to avoid hydraulic failure through osmotic regulation (O'Brien et al. 2015). In our study,

1   seedlings in constant high light did not show a trade-off between growth and a proportional change

2   in NSC concentration, providing some evidence that they invest into both growth and storage when

3   light access is optimal. However, hydraulic failure is most likely to occur under adverse conditions,

4   for example during phases of water-stress or increased growth. Since the seedlings in our pot

5   experiment showed an increase in growth and proportional storage as a response to a sudden gap

6   opening we assume that: (i) NSC is continuously metabolized during the growth phase as a direct

7   response of light demanders to the light increase and therefore depleted, or (ii) the higher

8   proportional change in carbohydrates of shade-tolerants is beneficial to later stages of the seedling

9   ontogentic development, otherwise a simultaneous relative increase in growth and storage at the

10   same time could be a more effective strategy. The first assumption may support the theory of

11   divergence in the regeneration niche, where the ecophysiology of functional group differs in the

12   response to a sudden gap opening (light niche divergence). The second assumption may support

13   ontogenetic niche shifts (Kitajima and Porter, 2008) in a constant race to gain access to the canopy

14   level.

15   Through a controlled gap opening, as can be observed in response to a sudden tree- or

16   branch-fall under natural conditions, we show that in this pot experiment light demanders tended to

17   allocate proportionally less resources into NSC, starch or WSC concentration compared to shade-

18   tolerants (including the generalist species). This led to further propose a trade-off between the

19   maximum growth rate and the proportional change in NSC concentration in response to a gap

20   opening that was supported across five out of the six species (including all light demanders and

21   shade-tolerants). A clear exception to this proposed trade-off was found in the response of *D.*

22   *lanceolata.* This species took an intermediary role by responding with a low maximum relative

23   growth rate and proportionally less NSC concentration. Interestingly, *D. lanceolata* also responded

24   to the gap opening with a significantly smaller increase in alditol concentration compared to all

25   other species. These ecophysiological responses of its proportional change in NSC and alditol

26   concentrations are the main arguments for identifying *D. lanceolata* as a generalist. The generalistic

19

1   response of *D. lanceolata* may not be surprising as this species is highly aromatic and young trees

2   produce a clear yellow resin know as 'oil of camphor' (Oldfield et al. 1998). We argue that the

3   investment into defense mechanisms to resist herbivory may play an important role for species that

4   do not follow the proposed trade-off in the present study (Paine et al. 2012b).

5   The functional role of alditols in dipterocarps remains unclear and further research will have

6   to address the movement of soluble sugars in response to acclimation. Würth et al. (2005) reported

7   that the relative share of mobile carbon compounds was less than 10% for carbohydrates other than

8   starch, sucrose, fructose and glucose for 17 species of adult tropical trees. Hence, it may be that the

9   observed iditol in the present study is only present at the seedling stage, where, depending on the

10   light condition, it contributed 3-47% (mean absolute concentration: 0.1-17.8 mg g^{-1}) to total NSC

11   concentration. An early study reports the occurrence of iditol in berries of mountain ash (*Sorbus*

12   *aucuparia)* which also shows ectomycorrhizal symbiosis, as is the case for dipterocarps, however

13   no indication of the physiological role was given (Plouvier 1963). In the present study, seedlings

14   that were translocated from high to low light showed proportionally lower iditol concentration

15   compared to seedlings that were constantly exposed to low light. This could suggest that iditol plays

16   a role in the adaptation of seedling metabolism in response to altered light levels, however little is

17   known about the preferential use of iditol compared to other WSCs. Iditol could also act as an

18   abiotic stress protectant when seedlings face adverse environmental conditions, for example if they

19   are exposed to a sudden gap or overshadowed by a faster growing competitor, after an insect or

20   pathogen attack (Renaud & Mauffette, 1991; Liu & Tyree, 1997), or as a result of limiting abiotic

21   conditions (Tattini *et al*., 1996). Since dipterocarps readily form ectomycorrhizas (Saner *et al*.,

22   2010; Brearley 2012), future studies should also test for the possible role of iditol between seedlings

23   and their associated ectomycorrhiza in response to light acclimation. As alditols were shown to

24   improve stress tolerance, this may yield novel insights into mechanisms of tree species coexistence

25   at the plant physiological level in tropical forests. Although these ideas remain speculative, the

26   authors argue that the light acclimation response of iditol in *D. lanceolata* should be further

1 examined to test the potential role as (i) a dynamic carbohydrate buffer to support seedling growth,

2 (ii) an abiotic stress protectant for adverse environmental conditions or (iii) an intrinsic component

3 of the dipterocarp-ectomycorrhizal fungi symbiosis. The role of individual carbohydrate

4 components needs be considered to understand how the diverse dipterocarp community

5 physiologically adapts to canopy gap dynamics.

6

7 **Conclusions**

8 In conclusion, we show through a simulated gap opening in a pot experiment that selected

9 dipterocarps can be grouped into light demanders that respond with increased growth and a greater

10 relative decrease in wood density, whereas shade-tolerant species and a generalist show a a greater

11 relative increase in NSC concentration, including starch and WSC. Alditols were identified across

12 all species and light levels and although their functional role remains unknown we observed that the

13 generalist *D. lanceolata* responded to the gap opening with a smaller increase in alditol

14 concentration compared to all other species. These findings emphasize that the understanding of the

15 light niche divergence of these species needs to be broadened and linked to their physiology to

16 support their effective use in large-scale forest restoration efforts.

17

21

1   iditol and five anonymous reviewers for helpful comments on the manuscript. This is paper no. 13

2   of the Sabah Biodiversity Experiment.

1   **References**

2   Agyeman VK, Swaine MD, Thompson J. 1999. Responses of tropical forest tree seedlings to

3   irradiance and the derivation of a light response index. Journal of Ecology 87:815–827.

4   Ashton PS. 1982. Dipterocarpaceae. Flora Malesiana 9:237–552.

5   Ashton PS. 2004. Dipterocarpaceae. In: Soepadmo E, Saw LG, Chung RCK (editors). Tree Flora of

6   Sabah and Sarawak. Volume 5. Sandakan, Kepong, Kuching (Malaysia): Sabah Forestry

7   Department, Forest Research Institute Malaysia and Sarawak Forestry Department.

8   Augspurger CK. 1984. Light requirements of neotropical tree seedlings - a comparative-study of

9   growth and survival. Journal of Ecology 72:777–795.

10   Baltzer JL, Thomas SC. 2007. Determinants of whole-plant light requirements in Bornean rain

11   forest tree saplings. Journal of Ecology 95:1208–1221.

12   Baraloto C, Forget PM. 2007. Seed size, seedling morphology, and response to deep shade and

13   damage in neotropical rain forest trees. American Journal of Botany 94:901–911.

14   Baraloto C, Goldberg DE, Bonal D. 2005. Performance trade-offs among tropical tree seedlings in

15   contrasting microhabitats. Ecology 86:2461–2472.

16   Barker MG, Press MC, Brown ND. 1997. Photosynthetic characteristics of dipterocarp seedlings in

17   three tropical rain forest light environments: a basis for niche partitioning? Oecologia

18   112:453–463.

19   Bloor JMG. 2003. Light responses of shade-tolerant tropical tree species in North-East Queensland:

20   a comparison of forest- and shadehouse-grown seedlings. Journal of Tropical Ecology

21   19:163–170.

22   Bieleski RL. 1982. Sugar alcohols. In: Loewus A. and Tanner W (editors). Encyclopedia of plant

23   physiology. Vol. 13a. Plant carbohydrates. I. Intracellular carbohydrates. Berlin (Germany):

24   Springer Verlag. p. 158–192.

25   Brearley FQ. 2012. Ectomycorrhizal associations of the Dipterocarpaceae. Biotropica 44:637–648.

1   Brokaw NVL, Scheiner SM. 1989. Species composition in gaps and structure of a tropical forest.

2   Ecology 70:538–541.

3   Brown N, Press M, Bebber D. 1999. Growth and survivorship of dipterocarp seedlings: differences

4   in shade persistence create a special case of dispersal limitation. Philosophical Transactions

5   of the Royal Society B-Biological Sciences 354:1847–1855.

6   Brown ND, Whitmore TC. 1992. Do dipterocarp seedlings really partition tropical rain-forest gaps.

7   Philosophical Transactions of the Royal Society of London Series B-Biological Sciences

8   335:369–378.

9   Canham CD. 1989. Different responses to gaps among shade-tolerant tree species. Ecology 70:548–

10   550.

11   Canham CD, Kobe RK, Latty EF, Chazdon RL. 1999. Interspecific and intraspecific variation in

12   tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia

13   121:1–11.

14   Chave J. 2005. Measuring wood density for tropical forest trees; A field manual for the CTFS sites.

15   Toulouse (France).

16   Clearwater MJ, Susilawaty R, Effendi R, van Gardeningen PR. 1999. Rapid photosynthetic

17   acclimation of *Shorea johorensis* seedlings after logging disturbance in Central Kalimantan.

18   Oecologia 121:478–488.

19   Connell JH. 1978. Diversity in tropical rain forests and coral reefs - High diversity of trees and

20   corals is maintained only in a non-equilibrium state. Science, 199:1302–1310.

21   Dalling JW, Winter K, Hubbell SP. 2004. Variation in growth responses of neotropical pioneers to

22   simulated forest gaps. Functional Ecology 18:725–736.

23   Denslow JS. 1980. Patterns of plant-species diversity during succession under different disturbance

24   regimes. Oecologia 46:18–21.

25   Denslow JS, Ellison AM, Sanford RE. 1998. Treefall gap size effects on above- and below-ground

26   processes in a tropical wet forest. Journal of Ecology 86:597–609.

1   Dietz KJ, Keller F. 1997. Transient storage of photosynthates in leaves. In: Pessarakli M (editor).

2   Handbook of photosynthesis. New York (USA): Marcel Dekker. p. 717–737.

3   Eschenbach C, Glauner R, Kleine M, Kappen L. 1998. Photosynthesis rates of selected tree species

4   in lowland dipterocarp rainforest of Sabah, Malaysia. Trees 12:356–365.

5   Givnish TJ. 1988. Adaptation to sun and shade - a whole-plant perspective. Australian Journal of

6   Plant Physiology 15:63–92.

7   Gustafsson M, Gustafsson L, Alloysius D, Falck J, Sauwai Y, Karlsson A, Ilstedt U. 2016. Life

8   history traits predict the response to increased light among 33 tropical rainforest tree

9   species. Forest Ecology and Management 362:20–28.

10   Hartshorn GS. 1978. Tree Falls and Tropical Forest Dynamics. Cambridge (UK): Cambridge

11   University Press. p. 617–638.

12   Hector A, Philipson CD, Saner P, Chamagne J, Dzulkifli D, O'Brien M, Snaddon JL, Ulok P,

13   Weilenmann M, Reynolds G, et al. 2011. The Sabah Biodiversity Experiment: a long-term

14   test of the role of tree diversity in restoring tropical forest structure and functioning.

15   Philosophical Transactions of the Royal Society B 366:3303–3315.

16   Huante P, Rincon E. 1998. Responses to light changes in tropical deciduous woody seedlings with

17   contrasting growth rates. Oecologia 113:53–66.

18   Hubbell SP, Foster RB. 1992. Short-term dynamics of a neotropical forest - Why ecological

19   research matters to tropical conservation and management. Oikos 63:48–61.

20   Kitajima K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates

21   of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428.

22   Kitajima K, Bolker BM. 2003. Testing performance rank reversals among coexisting species:

23   crossover point irradiance analysis by Sack & Grubb (2001) and alternatives. Functional

24   Ecology 17:276–281.

25   Kitajima K, Poorter L. 2008. Functional basis for resource niche partitioning by tropical trees. In:

26   Carson W, Schnitzer S (editors). Tropical Forest Community Ecology. Oxford (UK): Wiley-

27   Blackwell. P. 172-188.

1   Kobe RK. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling

2   survivorship and growth. Oikos 80:226–233.

3   Kobe RK, Pacala SW, Silander JA, Canham CD. 1995. Juvenile tree survivorship as a component

4   of shade tolerance. Ecological Applications 5:517–532.

5   Larjavaara M, Muller-Landau H. 2012. Still rethinking the value of high wood density. American

6   Journal of Botany 99:165–168.

7   Latham RE. 1992. Cooccurring tree species change rank in seedling performance with resources

8   varied experimentally. Ecology 73: 2129–2144.

9   Leakey ADB, Press MC, Scholes JD. 2003. Patterns of dynamic irradiance affect the photosynthetic

10   capacity and growth of dipterocarp tree seedlings. Oecologia 135:184–193.

11   Liu X, Tyree MT. 1997. Root carbohydrate reserves, mineral nutrient concentrations and biomass in

12   a healthy and a declining sugar maple (*Acer saccharum*) stand. Tree Physiology 17: 179–

13   185.

14   Loescher WH, Everard JD. 2000. Regulation of sugar alcohol biosynthesis. In: Leegood RC,

15   Sharkey TD and von Caemmerer S (editors). Photosynthesis: Physiology and metabolism.

16   Dordrecht (Netherlands): Kluwer Academic Publishers. p. 275–299.

17   Marthews TR, Burslem DFRP, Paton SR, Yangüez F, Mullins CE. 2008. Soil drying in a tropical

18   forest: Three distinct environments controlled by gap size. Ecological Modelling 216:369–

19   384.

20   McCready RM, Guggolz J, Silviera V, Owens MS. 1950. Determination of starch and amylose in

21   vegetables. Analytical Chemistry 22:1156–1158.

22   McDowell NG, Sevanto S. 2010. The mechanisms of carbon starvation: how, when, or does it even

23   occur at all? New Phytologist 186:264–266.

24   Moad AS. 1992. Dipterocarp sapling growth and understorey light availability in tropical lowland

25   forest. Cambridge (USA): Harvard University.

1   Muff S, Riebler A, Held L, Rue H, Saner P. 2014. Bayesian analysis of measurement error models

2   using integrated Laplace approximations. Journal of the Royal Statistical Society Series C

3   (Applied Statistics) 64:231–252.

4   Myers JA, Kitajima K. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in

5   a neotropical forest. Journal of Ecology 95:383–395.

6   Newman MF, Burgess PF, Whitmore TC. 1998. Manual of Dipterocarps for Foresters: Borneo

7   Island Medium and Heavy Hardwoods. Edinburgh (UK): Royal Botanic Garden Edinburgh

8   and CIFOR.

9   Nicieza AG, Alvarez D. 2009. Statistical analysis of structural compensatory growth: how can we

10   reduce the rate of false detection? Oecologia 159(1):27–39.

11 O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree

12   seedlings enhanced by non-structural carbohydrate levels. Nature Climate Change 4:710–

13   714.

14 O'Brien MJ, Burslem DFRP, Caduff A, Tay J, Hector A. 2015. Contrasting nonstructural

15   carbohydrate dynamics of tropical tree seedlings under water deficit and variability. New

16   Phytologist 205:1083–1094.

17 Oldfield S, Lusty C, MacKinven A. 1998. The World List of Threatened Trees. Cambridge

18   (UK):World Conservation Press.

19 Osunkoya OO, Ash JE. 1991. Acclimation to a change in light regime in seedlings of six Australian

20   rainforest tree species. Australian Journal of Botany 39:591–605.

21 Paine CET, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA. 2012a. How to fit

22   nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods

23   in Ecology and Evolution 3:245–256.

24 Paine CET, Stenflo M, Philipson CD, Saner P, Bagchi R, Ong RC, Hector A. 2012b. Differential

25   growth responses in seedlings of ten species of Dipterocarpaceae to experimental shading

26   and defoliation, Journal of Tropical Ecology 28:377–384.

Paine CET, Amissah L, Auge H, Baraloto C, Baruffol M, Bourland N, Bruelheide H, Daînou K, de
    Gouvenain R, Doucet J-L, et al. 2015. Globally, functional traits are weak predictors of
    juvenile tree growth, and we do not know why. Journal of Ecology 4:978–989.

Parsons WFJ, Knight DH, Miller SL. 1994. Root gap dynamics in lodgepole pine forest - Nitrogen
    transformations in gaps of different size. Ecological Applications 4:354–362.

Pausas JG. 2015. Bark thickness and fire regime. Functional Ecology 29:315–327.

Peters S, Mundree SG, Thomson JA, Farrant JM, Keller F. 2007. Protection mechanisms in the
    resurrection plant *Xerophyta viscosa* (Baker): both sucrose and raffinose family
    oligosaccharides (RFOs) accumulate in leaves in response to water deficit. Journal of
    Experimental Botany 58:1947–1956.

Peters S, Keller F. 2009. Frost tolerance in excised leaves of the common bugle (*Ajuga reptans* L.)
    correlates positively with the concentrations of raffinose family oligosaccharides (RFOs).
    Plant Cell and Environment 32:1099–1107.

Philipson CD, Saner P, Marthews TR, Nilus R, Reynolds G, Turnbull LA, Hector A. 2012. Light-
    based regeneration niches: evidence from 21 dipterocarp species using size-specific RGRs.
    Biotropica 44:627–636.

Philipson CD, Dent DH, O'Brien MJ, Chamagne J, Dzulkifli D, Nilus R, Philips S, Reynolds G,
    Saner P, Hector A. 2014. A trait-based trade-off between growth and mortality: evidence
    from 15 tropical trees species using size-specific relative growth rates. Ecology & Evolution
    4:3675–3688.

Pinheiro JC, Bates DM. 2000. Mixed-effects Models in S and S-Plus. New York (USA): Springer
    Verlag.

Plouvier V. 1963. Distribution of aliphatic polyols and cyclitols. In: Swain T (editor). Chemical
    plant taxonomy. New York (USA): Academic Press. p. 313–336.

Poorter L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative
   importance of morphological and physiological traits. Functional Ecology 13:396–410.

1   Poorter L. 2005. Resource capture and use by tropical forest tree seedlings and their consequences

2   for competition. In: Burslem DFRP, Pinard MA, Hartley SE (editors). Biotic Interactions in

3   the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge (UK):

4   Cambridge University Press.p. 35–64.

5   Poorter L, Kitajima K. 2007. Carbohydrate storage and light requirements of tropical moist and dry

6   forest tree species. Ecology 88:1000–1011.

7   Poorter L, Kitajima K, Mercado P, Chubiña J, Melgar I, Prins HHT. 2010. Resprouting as a

8   persistance strategy of tropical trees: relations with carbohydrate storage and shade

9   tolerance. Ecology 91(9):2613–2627.

10 Quentin AG, Pinkard EA, Ryan MG, Tissue DT, Baggett LS, Adams HD, Maillard P, Marchand J,

11   Landhäusser SM, Lacointe A, et al. 2015. Non-structural carbohydrates in woody plants

12   compared among laboratories. Tree Physiology 35:1146–1165.

13 R Development Core Team. 2015. R: A Language and Environment for Statistical Computing. R

14   Foundation for Statistical Computing. Vienna (Austria): R Foundation for Statistical

15   Computing.

16 Raich JW, Christensen NL. 1989. Malaysian dipterocarp forest: tree seedling and sapling species

17   composition and small-scale disturbance patterns. National Geographic Research 5:348–

18   363.

19 Renaud JP, Mauffette Y. 1991. The relationships of crown dieback with carbohydrate content and

20   growth of sugar maple (*Acer saccharum*). Canadian Journal of Forest Research 21:1111–

21   1118.

22 Rivier L. 2003. Criteria for the identification of compounds by liquid chromatography-mass

23   spectrometry and liquid chromatography-multiple mass spectrometry in forensic toxicology

24   and doping analysis. Analytica Chimica Acta 492:69–82.

25 Sabah Forestry Departement. 2008. A Guide to Plantation Forestry in Sabah. Sandakan (Malaysia):

26   Sabah Forest Departement.

1   Sack L, Grubb PJ. 2001. Why do species of woody seedlings change rank in relative growth rate

2   between low and high irradiance? Functional Ecology 15:145–154.

3   Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far

4   from being resolved. New Phytologist 186:274–281.

5   Saner P, Philipson CD, Ong RC, Majalap N, Egli S, Hector A. 2011. Positive effects of

6   ectomycorrhizal colonization on growth of seedlings of a tropical tree across a range of

7   forest floor light conditions. Plant Soil 338:411–421.

8   Saner P, Loh YY, Ong RC, Hector A. 2012. Carbon stocks and fluxes in tropical lowland

9   dipterocarp rainforests in Sabah, Malaysian Borneo. PLoS ONE, 7(1):e29642.

10   Symington CF. 1943. Foresters' Manual of Dipterocarps. Kuala Lumpur (Malaysia): Penerbit

11   Universiti Malaya.

12   Tattini M, Gucci R, Romani A, Baldi A, Everard JD. 1996. Changes in non-structural carbohydrates

13   in olive (*Olea europaea*) leaves during root zone salinity stress. Physiologia Plantarum 98:

14   117–124.

15   Valtat A. 2015. Tracking carbon use and allocation of non-structural carbohydrates in plant

16   response to drought. Zürich (Switzerland): University of Zürich.

17   Watling JR, Robinson SA, Woodrow IE, Osmond CB. 1997. Responses of rainforest understorey

18   plants to excess light during sunflecks. Australian Journal of Plant Physiology 24:17–25.

19   Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies

20   SJ, Diaz S, et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees.

21   Ecology 91:3664–3674.

22   Würth MKR, Pelaez-Riedl S, Wright SJ, Körner C. 2005. Non-structural carbohydrate pools in

23   tropical forest. Oecologia 143:11–24.

24   Wyatt-Smith J. 1995. Manual of Malayan Silviculture for Inland Forest. 2nd ed. Kuala Lumpur

25   (Malaysia): Forest Research Institute Malaysia.

1   Zipperlen SW. 1997. Ecophysiology of tropical rain forest tree seedlings (Dipterocarpaceae):

2   growth, gas exchange and light utilisation in contrasting light environments. Sheffield (UK):

3   University of Sheffield.

Figures
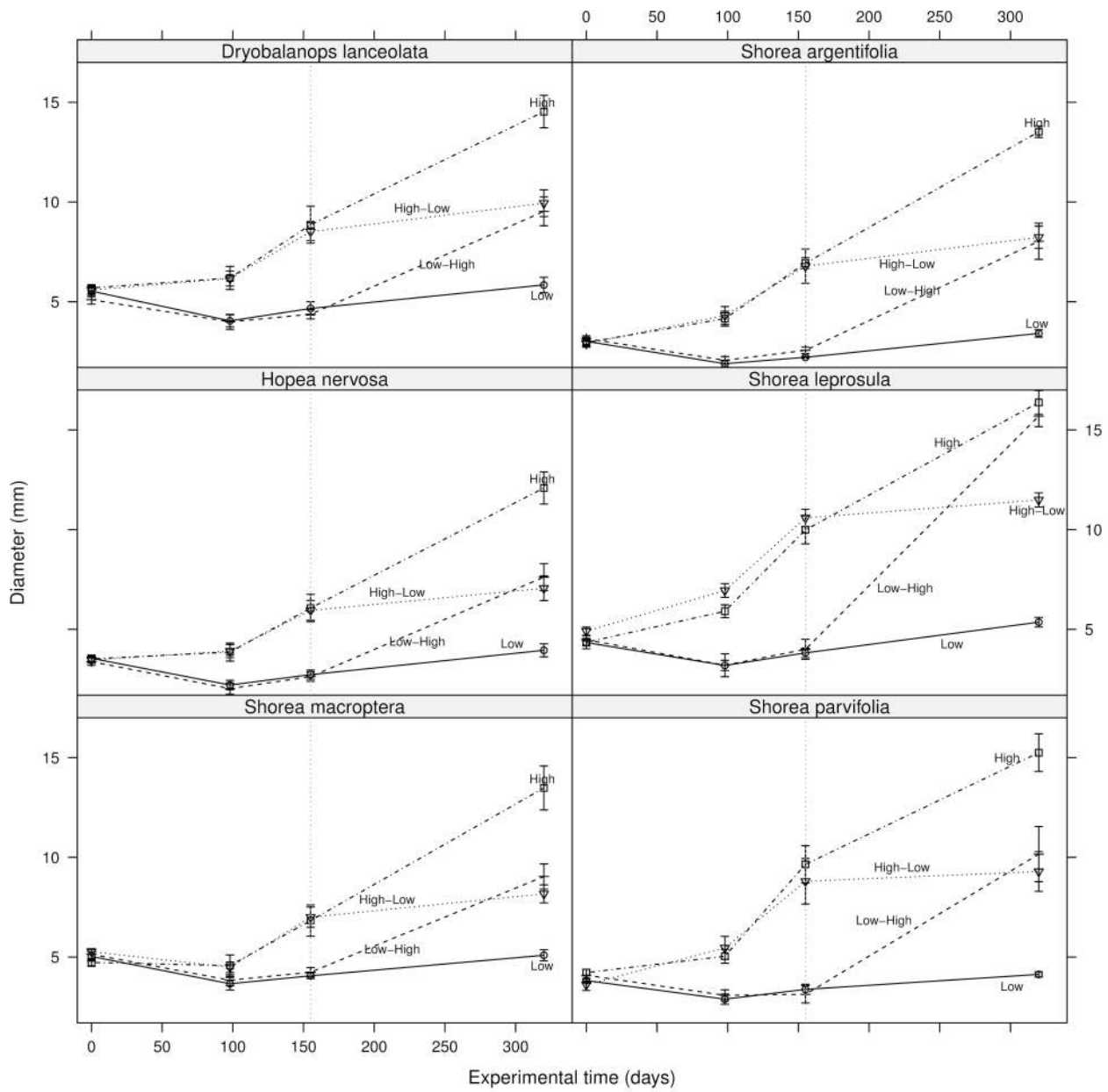
3 **Fig. 1.** Dipterocarp seedling growth over time under low- and high-light conditions grown in pots in

4 a shade-house. Seedlings of six species were non-destructively measured four times on day 0, 98,

5 155, 320. On day 155 (dotted line) seedlings were either kept under constant light condition (Low:

6 low-light, High: high-light) or switched between treatments (Low-High: low- to high-light, High-

7 Low: high- to low-light).
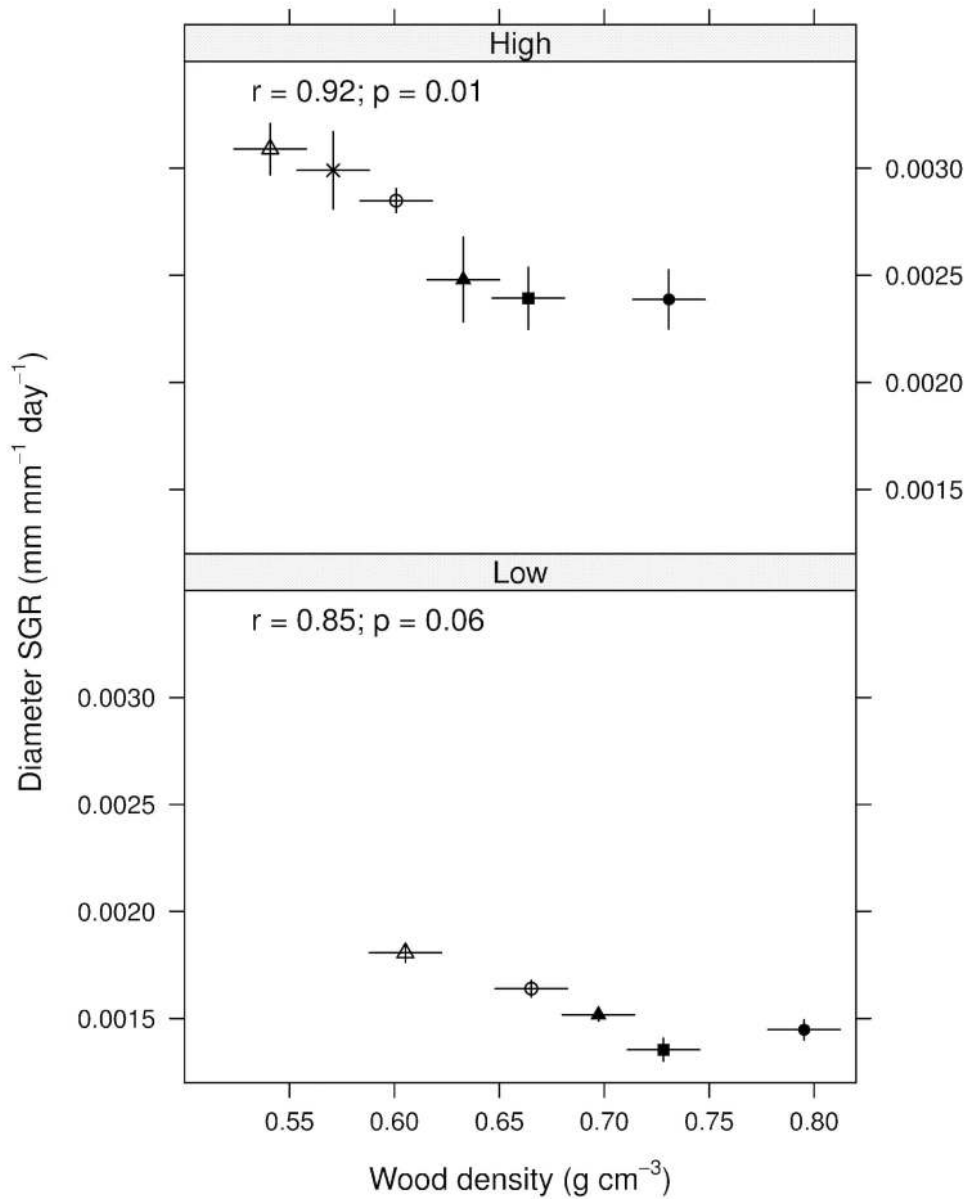
1

2 **Fig. 2.** Negative correlation across six dipterocarp species between mean (± SEM) size-specific

3 diameter growth rates (Diameter SGR) and wood density under high- and low-light condition

4 grown in pots in a shade-house. Open sympols represent the light demanders, full symbols represent

5 the shade-tolerants and the generalist. Low-light growth for *Shorea parvifolia* could not be

6 calculated and the species is therefore missing in the lower panel.

33
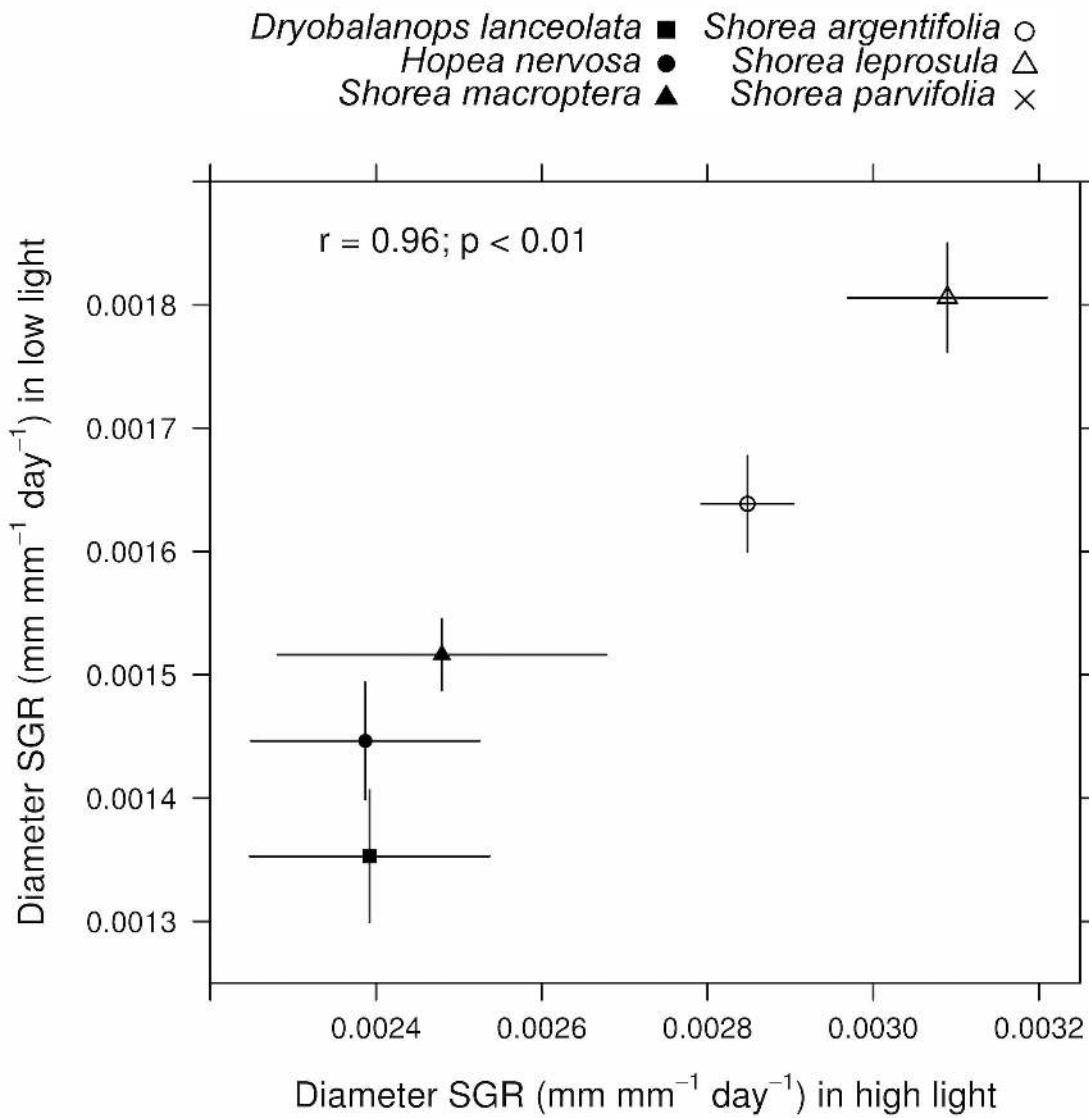
Fig. 3. Positive correlation across six dipterocarp species between mean (± SEM) size-specific diameter growth rates (Diameter SGR) in contrasting light conditions (high and low) grown in pots in a shade-house. Open sympols represent the light demanders, full symbols represent the shade-tolerants and the generalist. Low-light growth for *Shorea parvifolia* could not be calculated and the species is therefore missing.

1
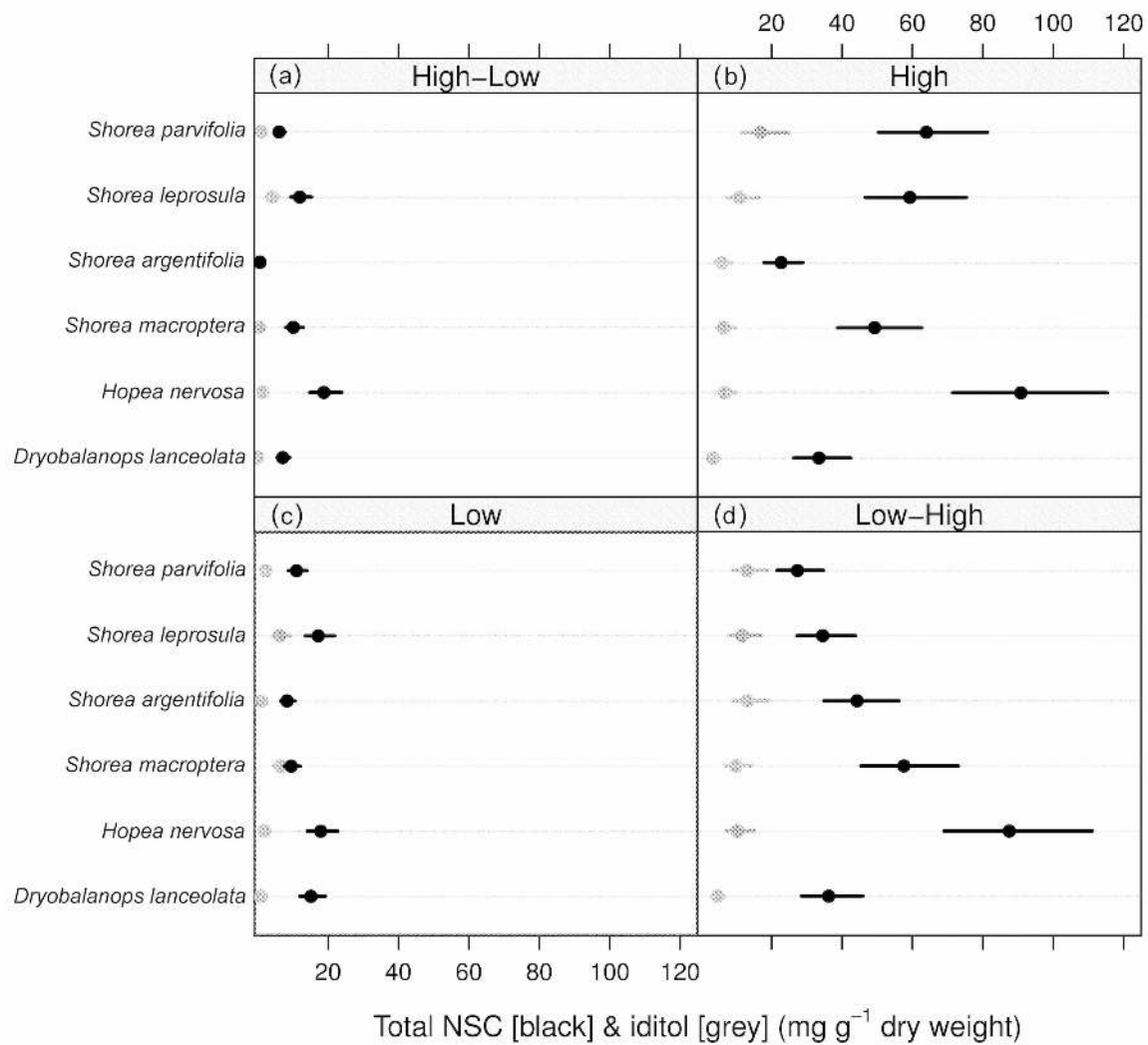
Fig. 4. Diperocarp seedlings adapt NSC concentration within five months to the surrounding light

conditions. NSC concentration (± SEM; mg g^{-1} dry weight) is reported as total NSC (black:

including starch and water soluble carbohydrates, WSCs) and for iditol separately (grey). Seedlings

were exposed to either constant high-light (b) or low-light (c) or translocated (a,d) half-way through

the experiment where they were grown in pots in a shade-house.
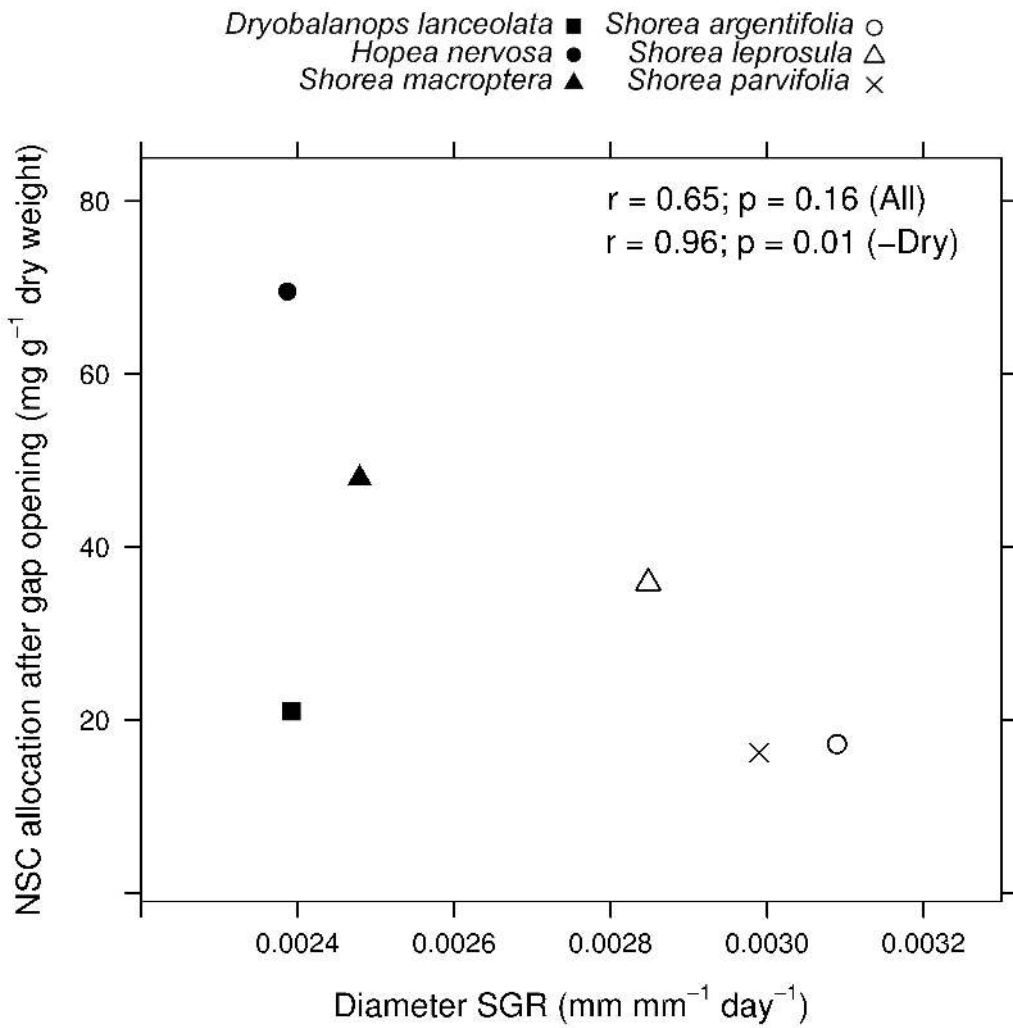
Fig. 5. Correlation between the proportional change in total NSC concentration (Δ NSC between low and low-high condition) after a simulated gap opening and the average species growth rate under high-light conditions across all six dipterocarp species grown in pots in a shade-house (All), and after removing *Dryobalanops lanceolata* (-Dry).
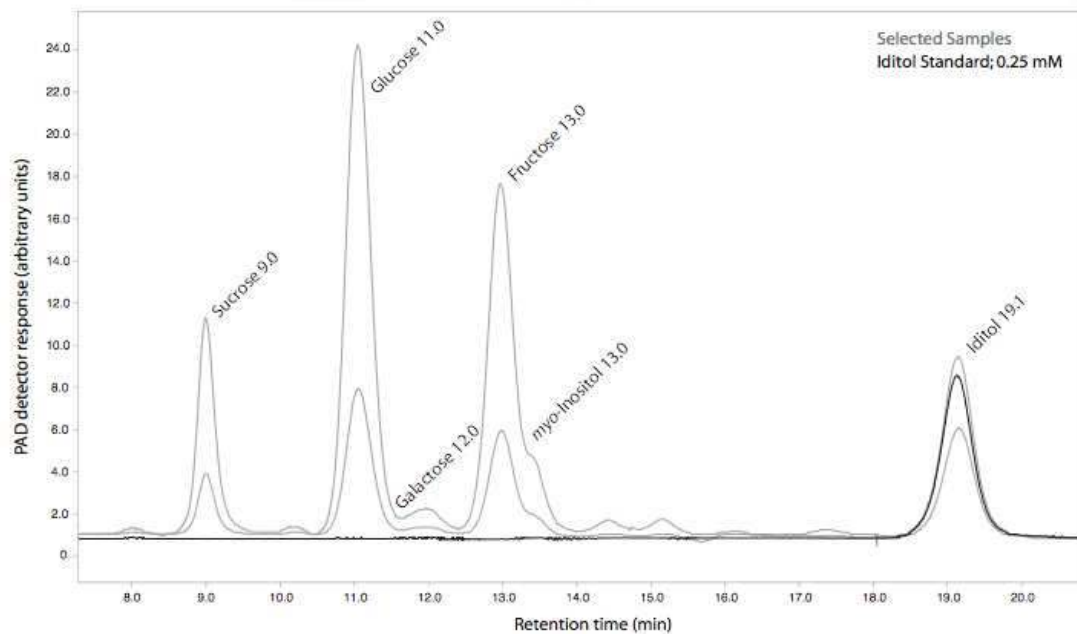
Figure S1 HPLC-PAD chromatograms of selected samples for the separation, identification and quantification of water-soluble carbohydrates (WSCs). The retention time of iditol (19.1 min) was similar to other alditols and the compound had to be further identified by GC/MS.

1

2

3

4

5

6

7

8

9

10

11

12

13

14

1 **Tables**

2 **Table 1** Overview of total NSC concentration for all six dipterocarp species in two constant (High,

3 Low) and two translocated (High-Low, Low-High) light conditions when grown in pots in a shade-

4 house. Mean ± SEM (mg g^{-1} dry weight) are reported for starch, total water-soluble carbohydrates

5 (WSCs), iditol and total NSC concentration. Note that iditol is included in WSCs and also reported

6 separately for ease of interpretation. Percentage of contribution to total NSCs is shown in

7 parentheses.

8

		Dryobalanops lanceolata		*Hopea nervosa*		*Shorea macroptera*		*Shorea argentifolia*		*Shorea leprosula*		*Shorea parvifolia*	
Low													
	Starch	5.0 ± 1.5	(29.9)	3.2 ± 1.6	(15.5)	4.4 ± 2.3	(31.2)	1.6 ± 0.4	(18.6)	2.8 ± 1.1	(14.8)	2.0 ± 1.2	(13.5)
	WSC	11.7 ± 2.6	(70.1)	17.4 ± 3.9	(84.5)	9.7 ± 3.1	(68.8)	7.0 ± 1.2	(81.4)	16.2 ± 3.6	(85.2)	12.8 ± 5.4	(86.5)
	Iditol	1.1 ± 0.2	(6.6)	2.1 ± 0.5	(10.2)	0.8 ± 0.2	(5.7)	2.2 ± 1.3	(25.6)	8.8 ± 3.0	(46.6)	4.7 ± 2.8	(31.8)
	NSC	16.7 ± 2.8	(100)	20.6 ± 5.4	(100)	14.1 ± 5.3	(100)	8.6 ± 1.1	(100)	19.0 ± 3.6	(100)	14.8 ± 5.7	(100)
Low-High													
	Starch	14.0 ± 3.9	(34.6)	47.5 ± 14.8	(50.2)	13.3 ± 3.1	(21.4)	7.0 ± 4.4	(16.1)	18.6 ± 1.3	(41.4)	8.0 ± 3.2	(28.2)
	WSC	26.4 ± 6.9	(65.4)	47.2 ± 6.6	(49.8)	48.7 ± 8.9	(78.6)	36.4 ± 6.4	(83.9)	26.3 ± 1.8	(58.6)	20.4 ± 4.0	(71.8)
	Iditol	5.4 ± 1.7	(13.4)	12.0 ± 2.6	(12.7)	10.8 ± 2.5	(17.4)	12.5 ± 2.4	(28.8)	13.7 ± 1.4	(30.5)	12.9 ± 1.7	(45.4)
	NSC	40.4 ± 10.6	(100)	94.7 ± 17.5	(100)	62.0 ± 11.4	(100)	43.4 ± 9.3	(100)	44.9 ± 1.2	(100)	28.4 ± 7.2	(100)
High-Low													
	Starch	5.0 ± 1.7	(56.2)	3.8 ± 1.4	(19.2)	2.7 ± 0.9	(24.1)	0.6 ± 0.2	(54.5)	5.1 ± 0.7	(40.5)	2.5 ± 1.1	(34.7)
	WSC	3.9 ± 1.2	(43.8)	16.0 ± 1.9	(80.8)	8.5 ± 2.0	(75.9)	0.5 ± 0.1	(45.5)	7.5 ± 1.4	(59.5)	4.7 ± 0.8	(65.3)
	Iditol	0.3 ± 0.1	(3.4)	1.9 ± 0.3	(9.6)	1.0 ± 0.3	(9)	0.1 ± 0.01	(9.1)	4.6 ± 0.8	(36.5)	1.6 ± 0.5	(22.2)
	NSC	8.9 ± 2.2	(100)	19.8 ± 2.8	(100)	11.2 ± 1.8	(100)	1.1 ± 0.3	(100)	12.6 ± 1.4	(100)	7.2 ± 1.7	(100)
High													
	Starch	16.5 ± 3.6	(48.8)	50.0 ± 15.2	(51.1)	15.1 ± 2.5	(29.7)	8.4 ± 3.7	(35.4)	35.0 ± 9.3	(57.8)	31.7 ± 7.6	(46.3)
	WSC	17.3 ± 2.1	(51.2)	47.9 ± 9.2	(48.9)	35.8 ± 6.3	(70.3)	15.3 ± 1.0	(64.6)	25.5 ± 5.4	(42.2)	36.8 ± 6.2	(53.7)
	Iditol	3.7 ± 0.1	(10.9)	7.7 ± 1.9	(7.9)	6.9 ± 0.9	(13.6)	6.2 ± 0.3	(26.2)	12.1 ± 2.4	(20)	17.8 ± 2.9	(26)
	NSC	33.8 ± 1.7	(100)	97.9 ± 18.3	(100)	50.9 ± 6.1	(100)	23.7 ± 3.3	(100)	60.5 ± 5.8	(100)	68.5 ± 11.5	(100)

9