

1 **Title**

2 Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in
3 response to light acclimation
4

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34

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36 The authors declare that they have no conflicts of interest. The authors acknowledge that they have
37 no financial interest or benefit arising from the direct applications of this research.
38

39 **Notes on Contributors**

40 **Philippe Saner** is an environmental scientist with a main interest in tropical plant community
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51 species are so different to each other, and what the consequences of these differences may be for
52 ecosystems.

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60

61 **Abstract**

62 **Background:** Light is a driver of tropical forest dynamics and key to understanding the coexistence
63 of dipterocarps, and how their key demographic rates and traits trade-off with acclimation to light.

64 **Aims:** Seedlings were expected to invest carbohydrates into denser wood at the cost of a lower
65 growth rate and to allocate resources to either growth or storage in response to light changes.

66 **Methods:** We examined the relationship between size-specific growth rates (SGR), wood density
67 and total non-structural carbohydrate (NSC) concentration under experimental shade house
68 conditions.

69 **Results:** Based on their functional response to light acclimation we grouped dipterocarps into light
70 demanders, shade-tolerants and a generalist species. Light demanders respond to a simulated gap
71 opening with increased growth, whereas shade-tolerants and the generalist show a higher relative
72 change in wood density and NSC concentration, including starch and water soluble carbohydrates.
73 Iditol—a hitherto unknown alditol in dipterocarps—was identified across all six species, and the
74 generalist responded to a gap opening with a significantly reduced relative change in alditol
75 concentration compared to light demanders and shade-tolerants.

76 **Conclusions:** Selected dipterocarps can be grouped into light demanders and shade-tolerants based
77 on their acclimation to light, however, the generalist species did not follow the proposed growth-
78 storage trade-off.

79

80 **Keywords**

81 Borneo, dipterocarps, NSC concentration, iditol, demographic rates, functional traits, size-specific
82 growth rate, light acclimation, shade-tolerants, light demanders

83

84 **Introduction**

85 The ecology of tropical tree species has been studied extensively at the seedling stage and in
86 response to light, a main driver of tropical forest dynamics (Augsburger 1984; Bloor 2003; Baltzer &
87 Thomas 2007; Baraloto & Forget 2007, Philipson et al. 2012, Paine et al. 2015). Some have tested
88 how seedlings respond to changes in light availability that occur during sudden gap formation or
89 closure caused by tree- or branchfalls in a natural forest (Osunkoya and Ash 1991; Parsons et al.
90 1994; Huante and Rincon 1998; Dalling et al. 2004; Philipson et al. 2014). Such events dramatically
91 alter both light availability and microclimatic conditions and offer a potential regeneration niche
92 axis along which species may be differentiated (Canham 1989; Denslow et al. 1998; Poorter 2005;
93 Marthews et al. 2008). Early theoretical concepts on the importance of canopy gap dynamic
94 processes and how they drive the coexistence of tree species, such as the gap size-niche partitioning
95 (Connell 1978; Hartshorn 1978; Denslow 1980) or cross-over point irradiance (Givnish 1988;
96 Latham 1992; Sack and Grubb 2001), were challenged for their over-simplicity (Brokaw and
97 Scheiner 1989; Raich and Christensen 1989; Brown and Whitmore 1992; Barker et al. 1997;
98 Agyeman et al. 1999; Brown et al. 1999; Kitajima and Bolker 2003; Baraloto et al. 2005). Mean
99 growth rate may be positively correlated between low-light and high-light conditions and thus show
100 no rank reversal in performance among species, however comparison of mean growth rate and
101 survival for the same species may still reveal a trade-off.

102 Subsequently, life history attributes were assessed, such as the ability to grow rapidly under
103 high-light environment of large canopy gaps, versus the ability to survive in low-light conditions
104 typical of the forest understory as a driving mechanism to promote species diversity (Hubbell and
105 Foster 1992; Kitajima 1994; Kobe et al. 1995; Poorter 1999). Sudden increases or decreases in light
106 may force a seedling to selectively allocate resources into structural tissue for current growth (e.g.
107 diameter) to outcompete others for access to light or, into denser wood or non-structural
108 carbohydrate (NSC) storage to prolong survival (Kobe 1997; Canham et al. 1999; Poorter et al.
109 2010). Again, this could reveal how an unpredictable resource—such as light in a tropical forest—

110 may promote coexistence by allowing species to partition forest light conditions (Myers and
111 Kitajima 2007; Poorter and Kitajima 2007).

112 The members of the *Dipterocarpaceae* (dipterocarps) family (Wyatt-Smith 1995) contribute
113 to about 50% of the upper canopy in undisturbed lowland mixed dipterocarp forest and comprise
114 the majority of commercial timber extracted from South East Asia (Symington 1943; Ashton 1982).
115 Dipterocarps offer an ideal study system to test these proposed trade-offs between investing into
116 mean growth rate or storage. They belong to the shade-tolerant climax species, but within this
117 general category have species specific differences based on their acclimation to light and wood
118 density (Gustafsson et al. 2016). Philipson et al. (2012) assessed trade-offs in growth rates of
119 dipterocarp seedlings and observed substantial crossovers among 21 species and no consistent
120 growth hierarchy across light treatments. This may indicate that the heterogeneity of the light
121 environment is a driving force to promote diversity in dipterocarps. Further, they assessed trade-offs
122 between mean growth rate and survival with a cross-comparison among 15 species—covering five
123 out of the six species in the present study—where the relationship in basal diameter growth and
124 probability of mortality was found to be positive (Philipson et al. 2014). In addition, this recent
125 study reported on a negative relationship between wood density and the probability of mortality,
126 suggesting that wood density can serve as a surrogate for survival in the dipterocarp seedlings of
127 this study.

128 Apart from the trade-off in structural tissue (growth and wood density) an additional key
129 trait that received attention lately is NSC. Recent findings on eight dipterocarp seedlings—including
130 four of the species of this study—show that NSC can be linked to increased survival under simulated
131 drought conditions (O'Brien et al. 2014, O'Brien et al. 2015). Further, soluble sugar concentration,
132 but not starch concentration, was reported to significantly increase in woody tissue and decrease in
133 leaf tissue of *Shorea beccariana* and *Shorea parvifolia* seedlings in response to a simulated drought
134 over 20 days (Valtat 2015). This shows that carbohydrates may fulfill diverse roles during plant
135 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 reducing power, 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 altered carbon balance in a shade house experiment. 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. The objective of this study was to test the following:

1. Relative changes in selected life history attributes in response to light acclimation allow for grouping dipterocarps into relative light demanders, shade-tolerants and a generalist species;
2. Shade-tolerants and the generalist species show a relative change in carbohydrates towards denser wood –a trait that positively correlates with survival– whereas light demanders increased their mean relative growth;
3. Shade-tolerants and the generalist, as a direct response to light acclimation, show an increased proportional change in carbohydrate concentration, whereas light demanders increase their mean relative growth.

Materials and methods

Experimental set-up

162 The study site (N05°05'20'' E117°38'32'', 102 m.a.s.l.) was located in the Malua Forest Reserve in
163 the eastern part of the Sabah province in Malaysian northern Borneo. The shade house experiment
164 is situated in logged lowland mixed dipterocarp forest, which is aseasonal with an annual rainfall of
165 approximately 3000 mm during the measurement period from 2004 to 2008 (Saner et al. 2012). Six
166 climax species native to Sabah and widely used for forest rehabilitation (Sabah Forestry Department
167 2008) were selected for this experiment based on their wood density (Newman et al. 1998) and
168 previous ecophysiological characterisation (Moad 1992; Zipperlen 1997; Clearwater et al. 1999):
169 *Dryobalanops lanceolata* Burck, *Hopea nervosa* King and *Shorea macroptera* Dyer, *Shorea*
170 *argentifolia* Sym., *Shorea leprosula* Miq. and *Shorea parvifolia* Dyer. Four of them are classified as
171 endangered (*D. lanceolata*, *S. argentifolia* and *S. leprosula*) or critically endangered (*H. nervosa*)
172 according to the IUCN red list (2015) and it is therefore essential to better understand their ecology.

173

174 *Study design*

175 The experimental design consisted of ten shade houses (4 x 6 x 5 m) that were aligned in five
176 blocks of two, randomly allocated to two light conditions. In order to minimize self shading, blocks
177 were sited along an east-west line with 3 m space between the houses and >10 m between blocks,
178 shade houses were covered with shade cloth on all sides. Within shade houses, seedlings were
179 spaced 0.3 m apart. To reduce the effect of herbivory, pots were located 0.3 m above ground and
180 surrounded by wire mesh to protect seedlings from mammal damage. Light conditions were
181 simulated by using either a single or triple layer of 70% black shade cloth to mimic respectively
182 (mean \pm SEM): a large gap (high; $32.9 \pm 4.5\%$ full sunlight; $127.5 \pm 13.2 \mu\text{mol m}^{-2} \text{s}^{-1}$), and the
183 forest understory (low; $2.6 \pm 0.6\%$ full sunlight; $11.7 \pm 2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$). Light conditions were
184 representative of the surrounding logged forest and slightly higher compared to previous studies due
185 to the degradation of shade cloth layers (Saner et al. 2011; Philipson et al. 2014).

186 All seedlings were grown from the seeds of wild fruiting trees and propagated under nursery
187 conditions ($\approx 11\%$ full sunlight) at the study site. To minimize intraspecific variation in initial size

we chose seedlings of the same age (18 months) and a similar height of approximately 0.5 m. Seedlings were transplanted into individual pots (0.3 x 0.4 m) using topsoil that was shredded to small pieces with a rotating conveyer belt (Royer Model 110, USA) to discharge stones and woody debris. In order to prevent roots from being damaged, seedlings were kept in the original soil while transplanting. Seedlings were watered twice daily (morning and late afternoon) to avoid drought stress and fertilized twice during the course of the experiment with 2.5 g Agroblen (Scotts PBG Malaysia Sdn. Bhd., Selangor, Malaysia) 6-month slow release fertilizer (16:8:9:3, N:P:K:Mg + trace elements). They were randomly relocated every month within each shade house to avoid positioning effects. Four individuals of each of the six species in every shadehouse (n=240) were present at the start in August 2006. On day 155, all seedlings in the low and high light shade houses were briefly moved into sunlit conditions. One individual per species from each shade house was then returned to the same light level, while the other was assigned to a new shade house with a different light level. This meant that half the seedlings experienced constant light conditions, either low or high for the entire experimental period, while the other half spent the first 155 days in either low or high light and the remaining 165 days in the opposite light treatment while controlling for the effect of movement between light treatments. Stem diameter (10 cm above ground) was measured at day 0, 98, 155 and 320 of the experiment (Figure 1). At day 320, all seedlings were harvested and oven-dried at 60°C for one week until constant mass, which likely lowered total NSC levels by oven drying. Wood density was measured for each individual plant by taking a wood sample from the lower stem following the water displacement method described in Chave (2005).

Seedling growth

Seedling growth rate analysis was done with the *nlme* package (Pinheiro and Bates 2000) in R 3.2.0 (R Development Core Team 2015). In order to estimate a seedling growth rate for each species that is unbiased by differences in initial size across species, we estimated size-specific diameter growth rates (SGR) (Nicieza and Alvarez 2009; Paine et al. 2012a). The growth rate was calculated by

214 fitting a non-linear power law of diameter against time for each individual seedling, for details on
215 the method see also Philipson et al. (2012; 2014). The growth rate was calculated for an average
216 diameter (5.8 mm) across all species half-way through the experiment.

217 Model convergence to estimate SGR could only be achieved for seedlings grown in constant
218 light conditions (low or high light) and which survived to the final harvest (79 individuals in total).
219 Non-linear models are more difficult to fit than linear models, and in this case problems were
220 compounded because some individuals simply did not grow in low light (Figure 1). To overcome
221 this problem a small number of seedlings ($n = 11$) from the low light condition were removed prior
222 to analysis, in particular, *S. parvifolia* was removed completely.

223 Power-laws can also be difficult to fit because of trade-offs among the three parameters: the
224 scaling exponent (α), the growth coefficient (β), and the initial diameter (M_0). We therefore decided
225 to restrict β to a single shared value among all species, which enabled us to fit individual growth
226 curves to all seedlings where predictions matched the raw data for constant light environments. The
227 selected model to estimate SGR included main effects of species ($F_{5,146} = 3.6$, $p < 0.01$) and light
228 (treated as continuous) ($F_{1,146} = 297.2$, $p < 0.0001$). The interaction was not significant and was
229 therefore not considered for calculating individual SGR. The best value of the growth coefficient β
230 was 0.1, indicating that the growth was almost linear (0 = linear; 1 = exponential).

231

232 *NSC and WSC analyses*

233 ~~Measuring total NSC by the phenol/sulphuric acid colorimetric assay is common in studies on~~
234 ~~tropical trees, seedlings and saplings (Yasman 1995; Ichie et al. 2005; Myers and Kitajima 2007).~~
235 ~~However, this conventional approach does not allow the relative contribution of single~~
236 ~~carbohydrates to be quantified (Hall 2003). Secondly, it is limited because (i) different~~
237 ~~carbohydrates yield different absorbances for the same amount of carbohydrate and (ii) sugar~~
238 ~~alcohols show only a very weak absorbance (Buyse and Merckx 1993). We used a more extensive~~

239 ~~approach (HPLC-PAD, GC/MS) to study the presence of water-soluble carbohydrates (WSC)~~
240 ~~separately (Ranwala and Miller 2008).~~

241 Analysis of NSC concentration was only carried out on seedlings growing in two light conditions
242 (high-light and low-light). Stem tissue from dipterocarp seedlings was shown to have slightly
243 higher concentrations of NSC compared to the roots or leaves (O'Brien et al. 2014), and wood
244 samples from the lower stem were used for carbohydrate analysis in the present study. However, as
245 the NSC extraction protocol of O'Brien et al. (2014, 2015) was different than in this study a direct
246 comparison of the NSC and WSC concentration may not be feasible (Quentin et al. 2015). Samples
247 were collected at the final harvest (day 320), transported to the laboratory on the collecting day and
248 oven-dried at 60°C for one week until constant mass. Samples of >1 g dry mass were ground to
249 fine powder in a ball mill (Tissue-Lyser, Qiagen, Germany).

250

251 *Extraction of WSC*

252 WSC were extracted twice in 1 ml of 80% and 20% ethanol (v/v), respectively, and twice in 1 ml
253 deionized water (dH₂O) (Peters et al. 2007). For each extraction, samples were heated at 80°C for
254 10 min, placed on ice for 2 min, and centrifuged (15,000 g, 5 min). The supernatants of all
255 extraction steps were pooled and adjusted to 6 ml with dH₂O. WSC (sucrose, glucose, fructose,
256 *myo*-inositol and alditols) were then separated, identified and quantified by HPLC-PAD (Peters and
257 Keller 2009). The remaining tissue was dried at 55°C to remove residual ethanol and subsequently
258 used to quantify starch. Representative WSC samples were tested for lipophilic substances using a
259 methanol-activated reverse-phase cartridge (C₁₈ Sep-Pak classic, 380 mg solid phase; Waters,
260 Rapperswil, Switzerland). The HPLC chromatograms of non-delipidated and delipidated extracts
261 were identical (data not shown), therefore we concluded that delipidation was unnecessary.

262

263 *Separation and quantification of WSC*

264 Aliquots (50 μ l) of WSC ethanol extracts were desalted and analyzed by HPLC-PAD (Peters &
265 Keller 2009). A Ca/Na-moderated ion partitioning carbohydrate column was used to separate WSCs
266 (Benson BC-100 column, 7.8 x 300 mm; Benson Polymeric, Reno, NV, USA). It was operated at
267 90°C and isocratically eluted with 0.005% (w/v) Ca/Na₂ – EDTA at a flow rate of 0.6 ml min⁻¹. The
268 BC-100 chromatographic system consisted of a Gynkotek model 480 High Precision Pump, a
269 Gynkotek Gina 50 autosampler and a Jones column temperature controller (Ercatech, Berne,
270 Switzerland). WSC were detected after post-column addition of NaOH (300 mM, 0.6 ml min⁻¹)
271 using an ESA Coulochem II electrochemical detector (ESA, Cambridge, MA, USA), operated with
272 an ESA 5040 analytical cell. WSC (sucrose, glucose, fructose, *myo*-inositol and alditols) were
273 quantified against a series of 5 nmol standard carbohydrates (Sigma Aldrich®, Switzerland). The
274 quantity of standard carbohydrates used corresponded to the linear response range of the
275 chromatographic system. An unknown alditol (retention time: 19.1 min) was compared to a series
276 of 5 nmol standard alditols (arabitol, erythritol, threitol, xylitol, mannitol, sorbitol, dulcitol and
277 iditol) (supplementary material Figure S1). However, the latter four hexitols showed similar
278 retention times (around 19 min), and the unknown alditol was thus further analyzed by GC/MS.

279

280 *Derivatization of alditol*

281 For derivatization of the alditol, the desalted and lyophilized samples (20 μ l) were dissolved in a
282 mixture of 40 μ l pyridine and 10 μ l trimethylsilyl imidazole (TMS). The solution was then heated
283 to 60°C for 30 min and 1 μ l injected into a Thermo Fisher Scientific (U.S.A.) gas chromatograph-
284 mass spectrometer (GC/MS) instrument consisting of a Trace GC and a single stage quadrupole MS
285 model DSQ. The split injector was at 250°C. The GC capillary column was DB5MS (J&W
286 Scientific, Folsom, CA, U.S.A.; 30 m x 0.25 mm i.d., 0.25 μ m film thickness) and was operated
287 from 60 to 300°C at a gradient of 8°C min⁻¹. Helium was used as carrier gas. The transfer line was
288 at 250°C. Mass spectra were recorded under electron impact at 70 eV, over the range 74 to 322 m/z
289 (mass-to-charge ratio) at one scan per second for the full scan mode. The chromatographic peaks

290 were identified by injection of pure compounds. Iditol was identified following Rivier (2003),
291 where the relative intensity $\geq 50\%$ of the base peak has an absolute tolerance of $\pm 10\%$, and for the
292 range between $< 50\%$ and $\geq 25\%$ the relative tolerance is $\pm 15\%$. Two fractions (217 and 319.1)
293 with the highest m/z could only be assigned to the iditol standard for eight random samples,
294 confirming that the alditol is indeed iditol (data not shown).

295

296 *Quantification of starch*

297 The Enzytec starch kit for food analysis was used to quantify starch (R-Biopharm, Germany).
298 Pellets were resuspended in 5 ml double distilled water and starch was gelatinized at 110°C for 30
299 min. Then, aliquots (20 μ l) were mixed with 20 μ l AGS containing α -amylglucosidase and α -
300 amylase and incubated at 60°C for 30 min. Aliquots (120 μ l) of dH₂O were added and remaining
301 plant debris removed by centrifugation (15,000 g, 10 min). Supernatant (120 μ l) was transferred
302 into the wells (total volume 323 μ l) of a microtiter plate (Greiner clear, Huber & Co AG,
303 Switzerland) and mixed with 80 μ l of solution #1 (containing NADP⁺) for the blank measurement.
304 The enzymatic reaction was initiated with 1.5 μ l of solution #2 (containing hexokinase and glucose-
305 6-phosphate dehydrogenase). Absorbance was measured after 6 min, at 2 min intervals (reaction
306 peak 14 min) at a wavelength of 340 nm. A glucose (Fluka[®], Switzerland) standard was used for
307 starch quantification; starch is expressed as glucose_{eq} (McCready et al. 1950). Quantification was
308 performed on a Spectra Max M2 plate reader (Bucher Biotec, Switzerland) using the SoftMax Pro
309 4.7.1 (Molecular Devices, Sunnyvale, CA, USA).

310

311 *Statistical analysis*

312 In a first step, as already described above in detail the individual seedling SGR was calculated with
313 a linear mixed-effects model. In a second step, individual seedling SGR, wood density and NSC
314 concentration (including starch, WSC and iditol) were then treated as dependent variables in a
315 second linear mixed-effects model and tested against species, functional groups and light treatment

316 (fixed effects). Shade house (n=5) and individual shade houses (n=10) were treated as random
317 effects. Where needed heteroscedasticity was controlled for by modelling increasing variance with
318 the varPower function, or in the case of total NSC concentration, starch and iditol concentration the
319 dependent variable was simply log transformed. In a third step Pearson's product moment
320 correlation was used to test for negative correlations between species mean values of SGR, wood
321 density, NSC concentration and iditol concentration. NSC concentration (%), but not pool size
322 (total mg), was included in the analyses.

323

324 **Results**

325 *Growth and wood density*

326 A significant main effect of wood density ($F_{1,35} = 121.4$, $p < 0.0001$), light condition ($F_{1,4} = 164.0$,
327 $p = 0.0002$) and functional groups ($F_{1,35} = 9.8$, $p = 0.0035$) on diameter SGR was observed. All
328 interactions were found to be non-significant. The negative correlation between mean diameter
329 SGR and mean wood density across all six species was found to be stronger in high light ($r = 0.92$,
330 $t = 4.6$, $df = 4$, $p = 0.01$, 95% CI: 0.99 to -0.41) compared to low light ($r = 0.85$, $t = 2.9$, $df = 3$, $p = 0.06$,
331 95% CI: -0.99 to 0.11) (Figure 2). Overall, a reduction in light increased wood density by 0.07 g
332 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 cm^{-3}).
333 Wood density was found to be significantly different between functional groups ($F_{1,48} = 28.0$,
334 $p < 0.0001$), however only a marginal interaction between light condition and functional groups ($F_{1,48}$
335 $= 3.6$, $p < 0.1$) was found.

336 A positive correlation ($r = 0.96$, $t = 6.3$, $df = 3$, $p < 0.01$, 95% CI: 0.55 to 1.00) was found
337 between species mean SGR in high-light and mean SGR in low-light conditions. Irrespective of
338 light conditions, the light demanders *S. argentifolia* and *S. leprosula* had a higher diameter growth
339 rate compared to the shade-tolerants *H. nervosa* and *S. macroptera* or the generalist *D. lanceolata*
340 (Figure 3).

341

342 *Relative change in NSC concentration and light acclimation*

343 Seedlings of all six species showed lower total NSC concentrations ($F_{1,4} = 60.9$, $p < 0.01$) in low-
344 light compared to the high-light condition and adjusted total NSC concentration within five months
345 of translocation (Figure 4a and d). Acclimation to a sudden light increase (gap opening) resulted in
346 a significantly different proportional change in total NSC concentration across species ($F_{5,20} = 3.2$, p
347 < 0.05). Overall the shade-tolerants (including the generalist species) showed a higher relative
348 change in NSC concentration compared to light demanders as a direct response to a simulated gap
349 opening ($F_{1,24} = 5.7$, $p < 0.05$). This is true for *S. leprosula* and *S. parvifolia*, however, *S.*
350 *argentifolia* was found to have increased relative NSC concentrations in response to the gap
351 opening (Figure 4b and d). NSC was further separated and analysed based on components, however
352 the finding was consistent with total NSC concentrations when testing for starch concentration ($F_{1,24}$
353 $= 4.7$, $p < 0.05$) or WSC concentration ($F_{1,24} = 4.0$, $p = 0.06$).

355 *Growth and storage*

356 The relationship between the proportional change in total NSC concentration after a gap opening (Δ
357 NSC between low and low-high condition) and the maximal average species growth rate under
358 high-light condition was further examined across species and functional groups (Figure 5). Overall,
359 we found no significant relationship between growth and storage across species. In particular, the
360 generalist *D. lanceolata* responded with a lower growth rate and a proportionally lower relative
361 change in total NSC concentration as a response to a gap opening. Once this species was excluded,
362 the relationship between the relative change in growth or storage was significant for the remaining
363 five species ($r = 0.96$, $t = 5.6$, $df = 3$, $p = 0.01$, 95% CI: -0.99 to -0.47). However, the light
364 demanders *S. argentifolia*, *S. leprosula* and *S. parvifolia* invested only marginally less to NSC
365 concentration compared to the shade-tolerants *H. nervosa* and *S. macropora* ($F_{1,3} = 7.6$, $p = 0.07$).

367 *Contribution of alditols to total NSC concentration*

WSC contributed 42–87% to total NSC concentration, depending on species and light condition (Table 1). A main component of WSC was identified as iditol, an alditol present in all six species and under all light conditions with a relative concentration compared to total NSC that ranged between 3–47% (mean absolute concentration: 0.1–17.8 mg g⁻¹) (Table 1). Despite the overall difference in iditol concentration between low light compared to high light conditions the interaction between treatment and species indicated that the increase was not significant for all species ($F_{5,40} = 2.4$, $p = 0.05$) (Figure 4b and c). However, seedlings across all six species adjusted iditol concentrations within five months to their present light condition, suggesting that the trait is highly adaptive (Figure 4a and d). Seedlings that were translocated from high to low light showed a significantly lower proportional change in iditol concentrations than seedlings that were constantly exposed to low light ($F_{1,4} = 29.5$, $p < 0.01$). Interestingly, the generalist *D. lanceolata* showed a significantly reduced relative change in iditol concentration as a direct response to a gap opening compared to all other species ($F_{1,24} = 15.8$, $p < 0.0001$). Correlation between iditol and other traits did not reveal any significant patterns across species and only an inconsistent pattern was observed within species where a negative relationship between the relative change in iditol concentration and wood density in the high light condition was found for three of the six dipterocarp species (*S. macroptera*, *S. argentifolia*, *S. leprosula*).

~~Across and within species comparison of traits in constant environments~~

~~NSC, WSC and iditol concentration in constant high light or low light conditions did not correlate significantly with growth in diameter SGR (supplementary material Figure S2 and S3) or wood density across species (supplementary material Figure S4 and S5). As the correlation between the relative concentration of iditol and wood density indicated a negative trend in the high light condition ($r=0.61$, $t=1.5$, $df=4$, $p>0.2$, 95% CI: 0.95 to 0.40), we further examined this relationship. The three-way interaction between the effect of wood density, light conditions and species on relative iditol concentration was not significant and therefore removed (likelihood ratio test: $\chi^2=$~~

3.2, $p = 0.68$). There was a significant two-way interaction between light conditions and species (likelihood ratio test: $\chi^2 = 22.2$, $p > 0.001$) suggesting that species had different levels of iditol concentration under altered light conditions. However, these differences were not clearly associated to functional groups (light demanders or shade-tolerators) in general.

Discussion

Clearly, the selection of species and the replication within each functional group does not represent the full ecological range with more than 250 species of dipterocarps for Borneo alone (Ashton 2004). However, based on changes in selected life history attributes in response to light acclimation we can group the six dipterocarp species into three relative light demanders (*S. argentifolia*, *S. leprosula* and *S. parvifolia*), two shade-tolerants (*Hopea nervosa* and *Shorea macroptera* and a generalist (*D. lanceolata*). Overall, light demanders show a higher relative change in growth and a decreased wood density compared to shade-tolerants (including the generalist species).

Investing into growth may be the single most important strategy for dipterocarps to escape the light limited environment of a tropical forest understory after a sudden gap opening (Gustafsson et al. 2016). However, in contrast to the findings of Philipson et al. (2012), who reported substantial crossovers among 21 species and no consistent growth hierarchy across light treatments, in the present study we found no crossovers in growth rates across light conditions and light demanders showed proportionally higher growth compared to shade-tolerants or the generalistic species. Wright et al. (2010) emphasized that seedlings that grow well in high light also show higher mortality in the dark. In dipterocarps this mechanism was reported lately, where the relationship in basal diameter growth and expected probability in mortality was found to be positive, and probability in mortality also negatively correlated with wood density (Philipson et al. 2014). Testing for a growth-mortality trade-off may require a negative carbon balance (Myers and Kitajima 2007). During our experiment, none of the seedlings in the experimental treatment died and although NSC concentration was low, it was not fully depleted even in low-light conditions and with little growth

over ten months. For example, *S. parvifolia* seedlings did not grow in low light and including that species into the analysis with a zero growth rate would weaken the consistent growth hierarchy across light conditions (Figure 3), although NSC concentration for this species was comparable to other species (Table 1 and Figure 4c). This reflects the ecology of dipterocarp seedlings, which are well known to be able to persist in the dark forest understorey close to their light compensation point for years (Watling et al. 1997; Eschenbach et al. 1998; Leakey et al. 2003). The relative change towards increased wood density across all species as a response to low-light conditions could suggest that wood density may be related to avoidance of structural damage for prolonged survival, as it has been proposed for bark thickness in response to fire regimes at the global scale (Pausas 2015). However, the functional role of a high wood density is yet unclear and a global assessment indicated only a weak negative relationship of wood density and sapling growth (Larjavaara and Muller-Landau 2012; Philipson et al. 2014; but see Paine et al. 2015).

As dipterocarps are well known to be highly resistant to adverse environmental conditions the proportional change in storage may support their prolonged survival under drought (O'Brien et al. 2014) and under light acclimation. By examining the proportional change in NSC and alditol concentrations, we include additional non-structural traits that have been proposed to be related to the life history strategies of tropical tree seedlings (Kobe 1997; Myers and Kitajima 2007; Poorter and Kitajima 2007; Poorter et al. 2010). Our results indicate that seedlings of selected dipterocarps respond to a sudden light increase with differing strategies and that the proportional change in NSC concentration is perhaps not only a reaction to resource limitation. Whereas some species show a higher relative change in growth to outcompete others in the race for canopy access, we found that they increase proportionally less in storage. We therefore argue that the exposure to sudden light changes and subsequent changes in storage levels—such as the response to a gap opening as described above—is a successful experimental approach to indicate life-history strategies and associated trade-offs in key functional traits.

445 Still, little is known about the functional role of NSC and its sub-components (starch and
446 soluble sugars) in dipterocarps. The results presented here are based on lower stem tissue only and
447 do not include root or leaf NSC concentration. However dipterocarp seedlings of the species
448 presented here were shown to have slightly higher but comparable concentrations of NSC in stem
449 compared to roots or leaves (O'Brien et al. 2014, but see Quentin et al. 2015). Carbohydrate
450 concentration in dipterocarps was found to increase during drought periods and especially soluble
451 sugars could be important to avoid hydraulic failure through osmotic regulation (O'Brien et al.
452 2015). In our study, seedlings in constant high light did not show a trade-off between growth and a
453 proportional change in NSC concentration, providing some evidence that they invest into both
454 growth and storage when light access is optimal. However, hydraulic failure is most likely to occur
455 under averse conditions, for example during phases of water-stress or increased growth. Since the
456 seedlings in our study showed a relative change in growth or proportional storage as a response to a
457 sudden gap opening we assume that, (i) NSC is continuously metabolized during the growth phase
458 and metabolic adaptation of light demanders as a response to the light increase and therefore
459 depleted, or (ii) the higher proportional change in carbohydrates in shade-tolerants is beneficial to
460 later stages of the seedling ontogenic development, otherwise a simultaneous relative increase in
461 growth and storage at the same time would be a more effective strategy.

462 Through a controlled gap opening, as can be observed in response to a sudden tree- or
463 branch fall under natural conditions, we show that light demanders tend to allocate proportionally
464 less resources into NSC, starch or WSC concentration compared to shade-tolerants (including the
465 generalist species). This led to further propose a trade-off between the maximum growth rate and
466 the proportional change in NSC concentration in response to a gap opening that was supported
467 across five out of the six species (including all light demanders and shade-tolerants). A clear
468 exception to this proposed trade-off was found in the response of *D. lanceolata*. This species took
469 an intermediary role by responding with a low maximum relative growth rate and proportionally
470 less NSC concentration. Interestingly *D. lanceolata* also responded to the gap opening with

471 significantly less proportional change in alditol concentration compared to all other species. These
472 ecophysiological responses of ist proportional change in NSC and alditol concentrations are the
473 main argument for identifying *D. lanceolata* as a generalist. The generalistic response of *D.*
474 *lanceolata* may not be surprising as this species is highly aromatic and young trees produce a clear
475 yellow resin know as 'oil of camphor' (Oldfield et al. 1998). We argue that the investment into
476 defense mechanisms to resist herbivory may play an important role for species that do not follow
477 the proposed trade-off in the present study (Paine et al. 2012b).

478 The functional role of alditols in dipterocarps remains unclear and further research will have
479 to address the movement of soluble sugars in response to acclimation. Würth et al. (2005) reported
480 that the relative share of mobile carbon compounds was less than 10% for carbohydrates other than
481 starch, sucrose, fructose and glucose for 17 species of adult tropical trees. Hence, it may be that the
482 observed iditol in the present study is only present at the seedling stage, where, depending on the
483 light condition, it contributed 3-47% (mean absolute concentration: 0.1-17.8 mg g⁻¹) to total NSC
484 concentration. An early study reports the occurrence of iditol in berries of mountain ash (*Sorbus*
485 *aucuparia*) which also shows ectomycorrhizal symbiosis, as is the case for dipterocarps, however
486 no indication on the physiological role was given (Plouvier 1963). In the present study, seedlings
487 that were translocated from high to low light showed proportionally less iditol concentration
488 compared to seedlings that were constantly exposed to low light. This could suggest that iditol plays
489 a role in the adaptation of seedling metabolism in response to altered light levels, however little is
490 known about the preferential use of iditol compared to other WSCs. Iditol could also act as an
491 abiotic stress protectant when seedlings face adverse environmental conditions, for example if they
492 are exposed to a sudden gap or overshadowed by a faster growing competitor, after an insect or
493 pathogen attack (Renaud & Mauffette, 1991; Liu & Tyree, 1997), or as a result of limiting abiotic
494 conditions (Tattini *et al.*, 1996). Since dipterocarps readily form ectomycorrhiza (Saner *et al.*,
495 2010), future studies should also test for the possible role of iditol between seedlings and their
496 associated ectomycorrhiza in response to light acclimation. As alditols were shown to improve

497 stress tolerance, this may yield novel insights into mechanisms of tree species coexistence at the
498 plant physiological level in tropical forests. Although these ideas remain speculative, the authors
499 argue that the light acclimation response of iditol in *D. lanceolata* should be further examination to
500 test the potential role as (i) a dynamic carbohydrate buffer to support seedling growth, (ii) an abiotic
501 stress protectant for adverse environmental conditions or (iii) an intrinsic component of the
502 dipterocarp-ectomycorrhizal fungi symbiosis. The role of individual carbohydrate components
503 needs be considered to understand how the diverse dipterocarp community physiologically adapts
504 to canopy gap dynamics.

505

506 **Conclusions**

507 In conclusion, we show through light acclimation experiments that selected dipterocarps can be
508 grouped into light demanders that show an increased relative change in growth, whereas shade-
509 tolerants and a generalist show a proportionally higher change into wood density and NSC
510 concentration, including starch and WSC. Alditols were identified across all species and light
511 levels. Although their functional role remains unknown we observed that the generalist *D.*
512 *lanceolata* responded to the gap opening with a significantly less proportional change in alditol
513 concentration compared to all other species. Our findings provide a novel insight into the ecology
514 of dipterocarps in response to light acclimation that deserves further attention.

515

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526 **References**

- 527 Agyeman VK, Swaine MD, Thompson J. 1999. Responses of tropical forest tree seedlings to
528 irradiance and the derivation of a light response index. *Journal of Ecology* 87:815–827.
- 529 Ashton PS. 1982. Dipterocarpaceae. *Flora Malesiana* 9:237–552.
- 530 Ashton PS. 2004. Dipterocarpaceae. In: Soepadmo E, Saw LG, Chung RCK (editors). *Tree Flora of*
531 Sabah and Sarawak. Volume 5. Sandakan, Kepong, Kuching (Malaysia): Sabah Forestry
532 Department, Forest Research Institute Malaysia and Sarawak Forestry Department.
- 533 Augspurger CK. 1984. Light requirements of neotropical tree seedlings - a comparative-study of
534 growth and survival. *Journal of Ecology* 72:777–795.
- 535 Baltzer JL, Thomas SC. 2007. Determinants of whole-plant light requirements in Bornean rain
536 forest tree saplings. *Journal of Ecology* 95:1208–1221.
- 537 Baraloto C, Forget PM. 2007. Seed size, seedling morphology, and response to deep shade and
538 damage in neotropical rain forest trees. *American Journal of Botany* 94:901–911.
- 539 Baraloto C, Goldberg DE, Bonal D. 2005. Performance trade-offs among tropical tree seedlings in
540 contrasting microhabitats. *Ecology* 86:2461–2472.
- 541 Barker MG, Press MC, Brown ND. 1997. Photosynthetic characteristics of dipterocarp seedlings in
542 three tropical rain forest light environments: a basis for niche partitioning? *Oecologia*
543 112:453–463.
- 544 Bloor JMG. 2003. Light responses of shade-tolerant tropical tree species in North-East Queensland:
545 a comparison of forest- and shadehouse-grown seedlings. *Journal of Tropical Ecology*
546 19:163–170.
- 547 Bieleski RL. 1982. Sugar alcohols. In: Loewus A. and Tanner W (editors). *Encyclopedia of plant*
548 physiology. Vol. 13a. Plant carbohydrates. I. Intracellular carbohydrates. Berlin (Germany):
549 Springer Verlag. p. 158–192.
- 550 Brokaw NVL, Scheiner SM. 1989. Species composition in gaps and structure of a tropical forest.
551 *Ecology* 70:538–541.

552 Brown N, Press M, Bebbler D. 1999. Growth and survivorship of dipterocarp seedlings: differences
553 in shade persistence create a special case of dispersal limitation. Philosophical Transactions
554 of the Royal Society B-Biological Sciences 354:1847–1855.

555 Brown ND, Whitmore TC. 1992. Do dipterocarp seedlings really partition tropical rain-forest gaps.
556 Philosophical Transactions of the Royal Society of London Series B-Biological Sciences
557 335:369–378.

558 Canham CD. 1989. Different responses to gaps among shade-tolerant tree species. Ecology 70:548–
559 550.

560 Canham CD, Kobe RK, Latty EF, Chazdon RL. 1999. Interspecific and intraspecific variation in
561 tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia
562 121:1–11.

563 Chave J. 2005. Measuring wood density for tropical forest trees; A field manual for the CTFS sites.
564 Toulouse (France).

565 Clearwater MJ, Susilawaty R, Effendi R, van Gardeningen PR. 1999. Rapid photosynthetic
566 acclimation of *Shorea johorensis* seedlings after logging disturbance in Central Kalimantan.
567 Oecologia 121:478–488.

568 Connell JH. 1978. Diversity in tropical rain forests and coral reefs - High diversity of trees and
569 corals is maintained only in a non-equilibrium state. Science, 199:1302–1310.

570 Dalling JW, Winter K, Hubbell SP. 2004. Variation in growth responses of neotropical pioneers to
571 simulated forest gaps. Functional Ecology 18:725–736.

572 Denslow JS. 1980. Patterns of plant-species diversity during succession under different disturbance
573 regimes. Oecologia 46:18–21.

574 Denslow JS, Ellison AM, Sanford RE. 1998. Treefall gap size effects on above- and below-ground
575 processes in a tropical wet forest. Journal of Ecology 86:597–609.

576 Dietz KJ, Keller F. 1997. Transient storage of photosynthates in leaves. In: Pessaraki M (editor).
577 Handbook of photosynthesis. New York (USA): Marcel Dekker. p. 717–737.

578 Eschenbach C, Glauner R, Kleine M, Kappen L. 1998. Photosynthesis rates of selected tree species
579 in lowland dipterocarp rainforest of Sabah, Malaysia. *Trees* 12:356–365.

580 Givnish TJ. 1988. Adaptation to sun and shade - a whole-plant perspective. *Australian Journal of*
581 *Plant Physiology* 15:63–92.

582 Gustafsson M, Gustafsson L, Alloysius D, Falck J, Sauwai Y, Karlsson A, Ilstedt U. 2016. Life
583 history traits predict the response to increased light among 33 tropical rainforest tree
584 species. *Forest Ecology and Management* 362:20–28.

585 Hartshorn GS. 1978. *Tree Falls and Tropical Forest Dynamics*. Cambridge (UK): Cambridge
586 University Press. p. 617–638.

587 Hector A, Philipson CD, Saner P, Chamagne J, Dzulkipli D, O’Brien M, Snaddon JL, Ulok P,
588 Weilenmann M, Reynolds G, et al. 2011. The Sabah Biodiversity Experiment: a long-term
589 test of the role of tree diversity in restoring tropical forest structure and functioning.
590 *Philosophical Transactions of the Royal Society B* 366:3303–3315.

591 Huante P, Rincon E. 1998. Responses to light changes in tropical deciduous woody seedlings with
592 contrasting growth rates. *Oecologia* 113:53–66.

593 Hubbell SP, Foster RB. 1992. Short-term dynamics of a neotropical forest - Why ecological
594 research matters to tropical conservation and management. *Oikos* 63:48–61.

595 Kitajima K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates
596 of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.

597 Kitajima K, Bolker BM. 2003. Testing performance rank reversals among coexisting species:
598 crossover point irradiance analysis by Sack & Grubb (2001) and alternatives. *Functional*
599 *Ecology* 17:276–281.

600 Kobe RK. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling
601 survivorship and growth. *Oikos* 80:226–233.

602 Kobe RK, Pacala SW, Silander JA, Canham CD. 1995. Juvenile tree survivorship as a component
603 of shade tolerance. *Ecological Applications* 5:517–532.

604 Larjavaara M, Muller-Landau H. 2012. Still rethinking the value of high wood density. American
605 Journal of Botany 99:165–168.

606 Latham RE. 1992. Cooccurring tree species change rank in seedling performance with resources
607 varied experimentally. Ecology 73: 2129–2144.

608 Leakey ADB, Press MC, Scholes JD. 2003. Patterns of dynamic irradiance affect the photosynthetic
609 capacity and growth of dipterocarp tree seedlings. Oecologia 135:184–193.

610 Liu X, Tyree MT. 1997. Root carbohydrate reserves, mineral nutrient concentrations and biomass in
611 a healthy and a declining sugar maple (*Acer saccharum*) stand. Tree Physiology 17: 179–
612 185.

613 Loescher WH, Everard JD. 2000. Regulation of sugar alcohol biosynthesis. In: Leegood RC,
614 Sharkey TD and von Caemmerer S (editors). Photosynthesis: Physiology and metabolism.
615 Dordrecht (Netherlands): Kluwer Academic Publishers. p. 275–299.

616 Marthews TR, Burslem DFRP, Paton SR, Yangüez F, Mullins CE. 2008. Soil drying in a tropical
617 forest: Three distinct environments controlled by gap size. Ecological Modelling 216:369–
618 384.

619 McCready RM, Guggolz J, Silviera V, Owens MS. 1950. Determination of starch and amylose in
620 vegetables. Analytical Chemistry 22:1156–1158.

621 McDowell NG, Sevanto S. 2010. The mechanisms of carbon starvation: how, when, or does it even
622 occur at all? New Phytologist 186:264–266.

623 Moad AS. 1992. Dipterocarp sapling growth and understorey light availability in tropical lowland
624 forest. Cambridge (USA): Harvard University.

625 Myers JA, Kitajima K. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in
626 a neotropical forest. Journal of Ecology 95:383–395.

627 Newman MF, Burgess PF, Whitmore TC. 1998. Manual of Dipterocarps for Foresters: Borneo
628 Island Medium and Heavy Hardwoods. Edinburgh (UK): Royal Botanic Garden Edinburgh
629 and CIFOR.

630 Nicieza AG, Alvarez D. 2009. Statistical analysis of structural compensatory growth: how can we
631 reduce the rate of false detection? *Oecologia* 159(1):27–39.

632 O’Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree
633 seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4:710–
634 714.

635 O’Brien MJ, Burslem DFRP, Caduff A, Tay J, Hector A. 2015. Contrasting nonstructural
636 carbohydrate dynamics of tropical tree seedlings under water deficit and variability. *New*
637 *Phytologist* 205:1083–1094.

638 Oldfield S, Lusty C, MacKinnon A. 1998. *The World List of Threatened Trees*. Cambridge
639 (UK):World Conservation Press.

640 Osunkoya OO, Ash JE. 1991. Acclimation to a change in light regime in seedlings of six Australian
641 rainforest tree species. *Australian Journal of Botany* 39:591–605.

642 Paine CET, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA. 2012a. How to fit
643 nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods*
644 *in Ecology and Evolution* 3:245–256.

645 Paine CET, Stenflo M, Philipson CD, Saner P, Bagchi R, Ong RC, Hector A. 2012b. Differential
646 growth responses in seedlings of ten species of Dipterocarpaceae to experimental shading
647 and defoliation, *Journal of Tropical Ecology* 28:377–384.

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

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

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

654 Peters S, Mundree SG, Thomson JA, Farrant JM, Keller F. 2007. Protection mechanisms in the
655 resurrection plant *Xerophyta viscosa* (Baker): both sucrose and raffinose family

656 oligosaccharides (RFOs) accumulate in leaves in response to water deficit. Journal of
 657 Experimental Botany 58:1947–1956.

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

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

664 Philipson CD, Dent DH, O’Brien MJ, Chamagne J, Dzulkifli D, Nilus R, Philips S, Reynolds G,
 665 Saner P, Hector A. 2014. A trait-based trade-off between growth and mortality: evidence
 666 from 15 tropical trees species using size-specific relative growth rates. Ecology & Evolution
 667 4:3675–3688.

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

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

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

674 Poorter L. 2005. Resource capture and use by tropical forest tree seedlings and their consequences
 675 for competition. In: Burslem DFRP, Pinard MA, Hartley SE (editors). Biotic Interactions in
 676 the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge (UK):
 677 Cambridge University Press. p. 35–64.

678 Poorter L, Kitajima K. 2007. Carbohydrate storage and light requirements of tropical moist and dry
 679 forest tree species. Ecology 88:1000–1011.

680 Poorter L, Kitajima K, Mercado P, Chubiña J, Melgar I, Prins HHT. 2010. Resprouting as a
 681 persistence strategy of tropical trees: relations with carbohydrate storage and shade
 682 tolerance. *Ecology* 91(9):2613–2627.

683 Quentin AG, Pinkard EA, Ryan MG, Tissue DT, Baggett LS, Adams HD, Maillard P, Marchand J,
 684 Landhäusser SM, Lacointe A, et al. 2015. Non-structural carbohydrates in woody plants
 685 compared among laboratories. *Tree Physiology* 35:1146–1165.

686 R Development Core Team. 2015. R: A Language and Environment for Statistical Computing. R
 687 Foundation for Statistical Computing. Vienna (Austria): R Foundation for Statistical
 688 Computing.

689 Raich JW, Christensen NL. 1989. Malaysian dipterocarp forest: tree seedling and sapling species
 690 composition and small-scale disturbance patterns. *National Geographic Research* 5:348–
 691 363.

692 Renaud JP, Mauffette Y. 1991. The relationships of crown dieback with carbohydrate content and
 693 growth of sugar maple (*Acer saccharum*). *Canadian Journal of Forest Research* 21:1111–
 694 1118.

695 Rivier L. 2003. Criteria for the identification of compounds by liquid chromatography-mass
 696 spectrometry and liquid chromatography-multiple mass spectrometry in forensic toxicology
 697 and doping analysis. *Analytica Chimica Acta* 492:69–82.

698 Sabah Forestry Departement. 2008. A Guide to Plantation Forestry in Sabah. Sandakan (Malaysia):
 699 Sabah Forest Departement.

700 Sack L, Grubb PJ. 2001. Why do species of woody seedlings change rank in relative growth rate
 701 between low and high irradiance? *Functional Ecology* 15:145–154.

702 Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far
 703 from being resolved. *New Phytologist* 186:274–281.

704 Saner P, Philipson CD, Ong RC, Majalap N, Egli S, Hector A. 2011. Positive effects of
705 ectomycorrhizal colonization on growth of seedlings of a tropical tree across a range of
706 forest floor light conditions. *Plant Soil* 338:411–421.

707 Saner P, Loh YY, Ong RC, Hector A. 2012. Carbon stocks and fluxes in tropical lowland
708 dipterocarp rainforests in Sabah, Malaysian Borneo. *PLoS ONE*, 7(1):e29642.

709 Symington CF. 1943. *Foresters' Manual of Dipterocarps*. Kuala Lumpur (Malaysia): Penerbit
710 Universiti Malaya.

711 Tattini M, Gucci R, Romani A, Baldi A, Everard JD. 1996. Changes in non-structural carbohydrates
712 in olive (*Olea europaea*) leaves during root zone salinity stress. *Physiologia Plantarum* 98:
713 117–124.

714 Valtat A. 2015. *Tracking carbon use and allocation of non-structural carbohydrates in plant
715 response to drought*. Zürich (Switzerland): University of Zürich.

716 Watling JR, Robinson SA, Woodrow IE, Osmond CB. 1997. Responses of rainforest understorey
717 plants to excess light during sunflecks. *Australian Journal of Plant Physiology* 24:17–25.

718 Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies
719 SJ, Diaz S, et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees.
720 *Ecology* 91:3664–3674.

721 Würth MKR, Pelaez-Riedl S, Wright SJ, Körner C. 2005. Non-structural carbohydrate pools in
722 tropical forest. *Oecologia* 143:11–24.

723 Wyatt-Smith J. 1995. *Manual of Malayan Silviculture for Inland Forest*. 2nd ed. Kuala Lumpur
724 (Malaysia): Forest Research Institute Malaysia.

725 Zipperlen SW. 1997. *Ecophysiology of tropical rain forest tree seedlings (Dipterocarpaceae):
726 growth, gas exchange and light utilisation in contrasting light environments*. Sheffield (UK):
727 University of Sheffield.

728 **Appendices**

729 Supplementary material:

730 **Figure S1** HPLC-PAD chromatograms of selected samples for the separation, identification and
731 quantification of water-soluble carbohydrates (WSCs).