Stem girth changes in response to soil water potential in lowland dipterocarp forest in Borneo: a time-series analysis

D. M. Newbery[1] and M. Lingenfelder[2]

Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

1. Corresponding author: david.newbery@ips.unibe.ch, ORCID iD 0000-0002-0307-3489.
2. Present address: Department of Biometrics and Computer Science, Forest Research Institute Baden-Württemberg, Wonnhaldestraße 4D, 79100 Freiburg, Germany

Last updated: 5 April 2021.

Abstract. Time series data offer a way of investigating the causes driving ecological processes. To test for possible differences in water relations between species of different forest structural guilds, daily stem girth increments (*gthi*), of 18 trees across six species were regressed individually on soil moisture potential (SMP) and temperature (TEMP), accounting for temporal autocorrelation (in GLS-arima models), and compared between a wet and a dry period. Coefficients were estimates of response in *gthi* to increasing SMP or TEMP. The best-fitting significant variables were SMP the day before and TEMP the same day. The first resulted in a mix of positive and negative coefficients, the second largely positive ones. Negative relationships for large canopy trees can be interpreted in a reversed causal sense: fast transporting stems depleted soil water and lowered SMP. Positive relationships for understorey trees meant they took up most water at high SMP. The unexpected negative relationships for these understorey trees may have been due to their roots accessing deeper water supplies (SMP being inversely related to that of the surface layer), and this was influenced by competition with larger neighbour trees. A tree-soil flux dynamics manifold may have been operating. Patterns of mean diurnal girth variation were more consistent among species than, but weakly related to, time-series coefficients, suggesting no simple trait-based differentiation of responses. Expected differences in response to SMP in the wet and dry periods did not support a previous hypothesis for drought and non-drought tolerant understorey guilds. Trees within species showed highly individual responses when tree size was standardized. Time-series *gthi*-SMP regressions might be applied as indicators of relative depth of access to water for small trees. Obtaining detailed information on individual tree's root systems and recording SMP at many depths and locations are needed to get closer to the mechanisms that underlie complex tree-soil water relations in tropical forests.

Keywords: stem girth increment, tropical rain forest, time series regression, soil moisture potential, drought response

INTRODUCTION

The influence of climatic perturbation by drought on rainforest tree dynamics has received increasing attention during the last decades, especially with the last major El Niño Southern Oscillation (ENSO) events in 1982/83, 1997/98 and 2015/16. Field studies of the phenomenon were conducted in South-East Asia by (Nakagawa et al. 2000, Harrison 2001, Aiba and Kitayama 2002, Potts 2003, Van Nieuwstadt and Sheil 2005, Vincent et al. 2009, Itoh et al. 2012). These forests experience a normally equable climate which is interrupted by infrequent strong dry spells. In Borneo ENSOs happen on average approximately once per 15 years (Walsh 1996, Walsh and Newbery 1999). Extensive studies have also been conducted in the Amazonia on the effects of ENSO related droughts (Phillips et al. 2009, Lewis et al. 2011), but the events are of a rather different nature as they come in addition to a regular intense dry season in that tropical region. Such climate perturbations in the long run form a process called environmental stochasticity.

Long-term research plots at Danum Valley in a primary lowland dipterocarp forest of Sabah, NE Borneo, have been maintained since 1985 in order to follow how the forest changed but also the effects of tropical climatic variability. They were enumerated four times, in 1986, 1996, 2001 and 2007, and forest dynamics recorded and analysed (Newbery et al. 1992, Newbery et al. 1996, Newbery et al. 1999, Newbery and Lingenfelder 2004, Lingenfelder and Newbery 2009, Newbery and Lingenfelder 2009, Newbery et al. 2011). In the first half of 1998 the forest at Danum was affected by unusually dry conditions associated with the 1997/98 ENSO, one of the strongest events on record for that part of the island. The usually aseasonal and continuously very wet climate (monthly rainfall 236 mm, (Newbery et al. 2011) was broken by a drought across almost two months between March and April 1998 with a 30-d running total of < 100 mm. Around the event the Oceanic Nino Index (ONI) was for 5 months > 2 (max. 2.4) (CPC 2020). An additional census on a subset of parts of the plots

in 1999 revealed that many trees were strongly affected by the lack of rainfall with especially decreases in stem growth rate (Newbery and Lingenfelder 2004).

The tree species in the ecosystem at Danum showed some evidence of adaptation to the moderate disturbance regime of occasionally severe droughts (Newbery et al. 1999, Walsh and Newbery 1999, Gibbons and Newbery 2003, Newbery and Lingenfelder 2004). The understorey is thought to play a key role in maintaining long-term structural stability via a feedback process in which species of the more numerous understorey species protect the smaller trees of overstorey ones, by keeping the forest microclimate favourable to them under the drought conditions (Newbery et al. 1999, Newbery et al. 2011, Newbery and Lingenfelder 2017). This model involves a mix of drought- and shade-tolerance among the understorey tree species leading to their different spatial distributions on the local topographic gradient (Newbery et al. 1996). The model does not necessarily imply any trade-offs in traits, and it does not concern the growth and survival of seedlings or saplings. Trees of the understorey species, those of ≥ 10 cm stem girth, whose growth was advanced in dry periods are hypothesized to have different ecophysiological responses to limiting water availability, and to increased light levels, from trees of understorey species that were not advanced and from those small trees of the overstorey species.

Moving closer to an understanding of the mechanisms that cause differences in effects of water limitation on tree growth across the species is not afforded by standard plot census monitoring with measurement intervals of 5-8 years. The clear 1996-1998 differences had narrowed and faded by 2001: the ‘memory effect’ was judged at 3-4 years (Newbery et al. 2011, Newbery and Lingenfelder 2017). A finer temporal resolution of stem size increment was required for a new period of dryness, preferably with a prior wet one for comparison. Unfortunately, against reasonable statistical expectation, another drought as severe as the 1997-1998 one did not occur by 2011. One of similar magnitude to 1997-98 did eventually

occur though within a 6-month period of 2015-2016 (ONI > 2, max 2.6). In 2007 the decision had to be taken to start daily recording of tree girth in the hope of catching one or more dry periods which would demonstrate effects of limitation of tree water availability. A moderate event in 2009-2010 did appear, and this allowed the analysis presented in this paper. Such considerations illustrate the precarious nature of field work involving environmental stochasticity operating at a scale of 1-2 decades. To have repeated events, i.e. a statistical sample over time, a century of recording might be just sufficient. The best prior indicators of a coming strong ENSO are at best 6 months ahead (Chen et al. 2004), and even that would not allow setting up a wet-period comparison beforehand.

Tree water relations can be explained to a large extent on the basis of physical laws (Monteith and Unsworth 1990, Jones 1992). How plants cope with limiting water supplies is today generally well understood, and this can be achieved with different mechanisms expressed collectively in the different species, in terms of their morphology and physiology, as traits (Zimmermann 1983, Tyree and Ewers 1991). Tree species with different ecologies are expected to show traits which are likely adaptive (Lambers et al. 1998). These traits, often quite complex though, may not be fully reducible to the detailed mechanisms but in their functioning they should show differences which are expressed as responses at intermediate or phenomenological level. One example is how stem girth changes in time as water (sap) fluxes through its active tissues and, at the same time, the stem grows incrementally. How this girth increment changes in respect of driving environmental factors may give an insight as to how different tree species, or guilds of species when their ecologies and traits are both similar, are adapted to variation in the demands and availability of water supply.

Several studies have demonstrated that tree girth fluctuation is closely correlated with water flux in the active xylem (e.g., (Kozlowski and Winget 1964, Herzog et al. 1995, Irvine and Grace 1997, Peramaki et al. 2001, Zweifel et al. 2006, Sevanto et al. 2008). Growth is

positively dependent on water supply – drought conditions tend to limit it. So in itself growth may not be easily separated from changes induced by water flux, though being only positive it will often be much smaller than the positive-negative flux on a *daily* basis. Growth may be expected to be non-linearly related, and temporarily lagged, to tree water status because it depends on cell metabolism.

Previous research on growth patterns of individual trees in tropical forests has shown the use of mechanical band dendrometers to be straightforward and generally reliable over time periods of months to years when they are used carefully (Pelissier and Pascal 2000, Sheil 2003, Stahl et al. 2010). More precise measurements of tree stem expansion and contraction though need electronic band dendrometers in order to record at a finer within- and between-day resolution (Drew and Downes 2009). Such instruments, with their electronic loggers, require intensive maintenance in the field under demanding humid tropical forest conditions. The alternative electronic point dendrometers require either mountings bolted into the wood, possibly causing damage to the stem or unnatural growth at the bolts (e.g., (Zweifel et al. 2006), or an invar steel frame with screws that can be difficult to operate on wet bark surfaces (e.g.,(Sevanto et al. 2008).

The present study aimed to follow stem size over time for six tree species at Danum (three under- and three overstorey), in a wet and a dry period, and to relate relative diurnal (= diel) changes, and daily increment time-series, to simultaneous recordings of soil moisture potential and ambient temperature. The question was whether species in the proposed drought-tolerant and -intolerant guilds showed different responses, in the directions predicted, and whether these differences were strong enough to support the suggested over-understorey dynamics model. For critically testing the following hypotheses state the expectations. (i) The rate of increase in daily girth increment with increasing soil moisture potential will be less steep for understorey than overstorey species as small trees. (ii) As soil moisture potential

decreases, drought-tolerant understorey species will have smaller reductions in daily girth increment than drought-intolerant ones. (iii) Drought-tolerant understorey species will be less affected in terms of daily girth increment in dry compared to wet periods than drought-intolerant understorey and small trees of the overstorey. It is further possible that there was a gradient in drought tolerance across understorey species, or within species an appreciable variation between individuals with respect to water stress that masks species differences.

STUDY SITE

This research was conducted in permanent forest dynamics plots within the Danum Valley Conservation Area, in Sabah, Malaysia. The site is situated in lowland dipterocarp forest, c. 70 km east of the town of Lahad Datu on north-eastern Borneo. The climate is ever-wet and aseasonal, with on average 2881 mm/yr rainfall (1985 – 2011; www.searrp.org). During the study period 6 March 2007 to 4 December 2010, mean daily rainfall was 8.110 ± 0.37 mm (n = 1370), mean dry bulb temperature at 14:00 h was 30.250 ± 0.068 ^{o}C (n = 991), and mean relative humidity at 14:00 h was 79.65 ± 0.28% (n = 983).

Two main 4-ha plots had been fully enumerated in 1986, 1996 and 2001, for all trees with stem girth (*gbh*) ≥ 10 cm (or 3.1 cm dbh, diameter at breast height). Their SW corners lay at 2008 and 220 m a.s.l., and each had a topographic gradient, lower-slope-to-ridge of ca. 35 m elevation. More details on the site and the plots can be found in (Newbery et al. 1992, Newbery et al. 1996, Lingenfelder and Newbery 2009). The present study used continuous (or ‘electronic’; eDDS) bands. They were not fixed into the wood and therefore caused no interference to tree growth.

To find trees suitable for the dendrometers, data from the 2001 enumeration were used. Six common species that showed responses to the 1998 drought (three understorey, and three overstorey, Table 1), were sought from both ridge and lower slope locations (Newbery

et al. 1996, Gibbons and Newbery 2003) in the main plots. Trees ≥ 10 cm diameter (*dbh*), or 31.42 cm girth (*gbh*) with intact stems and crowns were selected although some did have slightly smaller *dbh*-values. For ease of direct reference to previous papers for the site, *gbh* rather than *dbh* will be used for stem size.

METHODS IN FIELD

Selection of tree species

Within a list of 34 most abundant species (≥ 100 trees; (Newbery and Lingenfelder 2009) four were canopy-emergent species in the Dipterocarpaceae, the dominant, defining family in terms of basal area and the second most abundant in terms of stem density at Danum (Newbery et al. 1992, Newbery et al. 1996). Three of these dipterocarps showed strong responses to the 1998-drought: *Shorea parvifolia* decreased in relative growth rate (*rgr*) by *c*. 14% after the drought, but still had the highest *rgr* of all of the most abundant species; *Shorea fallax* was severely and persistently affected by the drought, dropping in *rgr* by 50% below the pre-drought value; *Parashorea malaanonan* was the only dipterocarp of the most abundant species to increase its *rgr* from the period 1986-1996 into the period 1996-2001; *Shorea johorensis*, however, showed little response (Newbery and Lingenfelder 2009). The former three species were therefore selected as the representatives of the overstorey species.

Abundant understorey species that showed strong responses to drought conditions include the ridge specialist *Cleistanthus contractus* (Euphorbiaceae; the most abundant family, 2nd-ranked in terms of basal area), but this species had too few trees ≥10 cm *dbh* available for sampling (these being located exclusively on the ridge of one plot). The other species that seemed to be adapted to ridges, and to be able to cope with drought-stress, is *Lophopetalum beccarianum* (Celastraceae), which was relatively unaffected during, and yet showed resilient growth after, the 1998 drought. The two most numerous species of the list of

34 were also included due to their importance in forming the understorey at Danum: *Dimorphocalyx muricatus* (Euphorbiaceae), another ridge specialist, which recovered strongly in growth, displaying a four-fold increase in *rgr* after the drought, and *Mallotus wrayi* (Euphorbiaceae), ubiquitous in both plots, which also recovered its growth (Newbery and Lingenfelder 2004, 2009). The latter three species were accordingly selected to represent the understorey species. Tag reference numbers identify the trees among the complete long-term census data. As explained later, bands on two of the 20 trees (g13, g21) were dropped.

Plot locations, species' distributions and characteristics of the sampled trees are shown in Fig. 1 and Tables 1 and 2. Crown status was assessed in March 2009 and February 2010 for the variables layer, space and light each on a scale of 1 to 5. Layer was scored (in increasing order) as treelet, understorey, mid-level, top canopy and emergent tree; space (with regard to neighbours) as completely suppressed, mixed and entangled crowns, significantly competing, crowns just touching, crowns free; and light as < 30, ≥ 30 - < 50, ≥ 50 - < 70, ≥ 70 - < 90 and ≥ 90 % of full light received by crown. These scores were averaged over the two dates to give a composite variable called CanStat. Thirteen trees had unchanged CanStat values between dates, for three they decreased, and for only two they slightly increased.

Set-up of continuous bands (eDDS)

Continuous dendrometer-bands (type 'D6'; UMS, Munich, Germany) were installed 05.-08.03.2007. The device consists of an Invar-steel measuring cable with a strain-gauge sensor clip, placed around a tree and resting on a Teflon-net to minimize friction (resolution of 5 µm gbh; dependence on temperature < 4 µm/K). In plot 2, bands were fitted to 20 trees of the six species, these being selected from a larger stratified random sample of 234 candidates considered for an *in situ* parallel study with conventional mechanical dendrobands to be reported elsewhere (Table 1). Plot 2 alone was used because the required numbers of trees within reasonable cable-length distances (maximum 20 m) to loggers were more suitable than

in plot 1. The trees were therefore not fully at random in the plot as they were necessarily clustered around the four loggers.

Bands were distributed across four stations (two lower slope, two ridge; Fig. 1). Each was equipped with a data-logger (CR10X; Campbell Scientific Inc., Logan, USA). On tree number 3, band g13 broke in the wet period, and there was long interval of no data whilst it was under repair; so no 'wet' means and limits were found. For tree number 6 (band g21) the tree died early on, and hence there were neither wet- nor dry-period data. One tree at station 2 (*S. parvifolia*) died early on in the study. Each station also had three to four soil equitensiometers (EQ2; Delta-T Devices Ltd, Cambridge, UK) installed, at a depth of *c*. 20 cm below ground surface, within a 10-m radius of loggers, to enable fluctuations in stem size to be related to soil water potential. Logger temperature was simultaneously recorded. The SMP correction for logger temperature, T (^{o}C), was $-$ (T$-$20)/4 in kPa, i.e. ~ 2.5 kPa or 2%.

Measurements made by tree and soil sensors were recorded automatically at 10-min intervals, and the half-hour averages logged. Stations were downloaded every *c*. 4 wk. During the first 3 yrs, only minor difficulties were experienced (one slight disturbance by elephants, some cable damage by termites, broken fuses due to occasional lightning strikes). In 2010 problems became more frequent and serious, and accordingly there became larger gaps in the time-series. In October 2010 two stations were attacked by elephants, which resulted in severe damage to loggers and sensors so that the study had to be terminated by December 2011.

DATA ANALYSIS

Analysis of eDDS and SMP data

Dendroband records on trees and SMP values each spanned slightly different times for the four stations, and within stations there were differing periods of missing days. All data

were first matched to a common time frame of 1614 days (48 half-hour points within each day) between 01.03.2007 and 31.07.2011 (Fig. 2). If an incidental or consecutive pair of values was missing, they were substituted by the means of values immediately before and after them. Daily means, of girth (cm) for each of the n = 20 trees, and of SMP (kPa) for the three or four soil sensors at each of the four stations, were found; and this allowed an identification of the complete, or nearly complete, periods of measurement. One long 'wet' period of 18 months (550 days), 17.03.2007 to 16.9.2008, had very few missing SMP-values (one of 15 days at station 3 and two of six and seven days at station 2), and the spectrum of SMP-values was fairly constant over time and similar across stations. SMP rarely fell below –50 kPa and on only five days < −100 kPa. There were 3-4 short periods of about 20 days later in 2008-09 which had complete 'wet' records but these were in amongst numerous repeatedly failing sensor runs, and showing a curious lack of a spectrum typical of the 18-month period indicated they were likely to have been unreliable throughout. However, a 3-month period, from 17.2.2010 to 16.5 2010, included three distinct yet short dry spells. These were clearly reproduced at each of the four stations, although stations 2 and 3 had a few days missing, and station 4 had a strange recording anomaly for 2 weeks.

The SMP values were handled in two ways to improve their robustness in defining wet and dry periods. Because of the existence of many small positive values of SMP after the conversion from logged date/time equipotentials to kPa, values were adjusted by subtracting the (upper) 0.95-quantile (per sensor) and the remaining positive values set to zero. These were called 'offset' SMP-values. Further, occasionally very low potentials (down to c. −2 MP), introduced by the fourth sensors at each station, appeared unrealistic. SMP-values were therefore truncated at the extremes: those positive were set to zero, and those very low values rounded up to −1000 kPa. These were called 'strict' SMP-values.

Stations 1 and 2 were 'LS' (lower slope) and stations 3 and 4 'R' (ridge) in the topographic classification (Fig. 1), and averaging these pairs' SMP-values fortunately allowed almost complete runs of data over the 3 months, and afforded a useful comparison with an earlier study. (Gibbons and Newbery 2003) had recorded SMP at 'LS' and 'R' locations within the same plots (slightly different sample layout) and built models to predict it from daily rainfall. SMP had then been measured with calibrated glass psychrometers. These last instruments are more reliable than the equitensiometers used in the present study, especially for lower potentials. The authors found a weighted rainfall index per day defined as $w_{40} = {}_{n=1}\Sigma^{40} (r_n/n)$, i.e. the sum of the preceding 40 days' rain and each weighted by its day number (e.g. $n = 1$ for the day before). This led to two equations (w_{40} in cm; SMP in MPa): one for 'LS', $SMP = -0.0096 - 1.4070b^{w40}$; the other for 'R', $SMP = -0.0525 - 2.0280b^{w40}$, with $b = 0.7554$. The equations were applied to the complete rainfall series at Danum, and for this study between 01.03.2007 and 30.07.2011 to give 'predicted' SMP at the 'LS' and 'R' stations, and thereby match the (non-missing) observed equitensiometer values.

Comparisons between the two approaches to adjusting SMP-values and their comparison with predicted values led to two clear results. (1) For 'LS' and 'R' (averaging SMP-values across the two stations each), 'offset' and 'strict' SMP-values were closely and similarly related. SMP-values were first transformed as $SMPtr = \sqrt{|SMP|}$ (e.g. −150 kPa becomes 12.25), and allowing the lower (more negative) original values (now relatively more positive transformed ones) to weight accordingly against the many low and near-zero values, the linear regressions were $SMPtr_{LS} = 3.46 + 0.889\ SMP_{LS}$ ($R^2 = 91.5\%$, $n = 1350$) for 'LS', and $SMPtr_R = 3.27 + 0.890\ SMP_R$ ($R^2 = 90.4\%$, $n = 1248$) for 'R'. Substituting an 'offset' threshold SMP = −150 kPa in these equations gives after back-transformation 'strict' thresholds of −97.9 and −101.8 kPa respectively. Hence, a threshold of −150 kPa with 'offset' translates to −100 kPa with a 'strict' setting. (2) Regressing 'offset' and 'strict' SMP-values

against w_{40}-predicted SMP (days where the latter was ≤ − 50 kPa for 'L', ≤ − 100 kPa for 'R'; *n* = 89 and 94 respectively) showed significant, though not particularly strong, quadratic relationships (R^2-values of 57.3 to 67.0%). 'Offset' SMP-values gave much closer to w_{40}-predicted values than 'strict' ones at 'LS' (the latter underestimating by c. 20%), whilst both 'offset' and 'strict' (more so) underestimated w_{40}-predicted values at 'R', by c. 30 and 45% respectively. It seems then that SMP-values on ridges were likely, in reality, to have been lower (taking the psychrometer values too as being the more reliable) than those recorded by the equitensiometers.

Dry periods were therefore defined as runs of (> 3 days) with 'LS'- and 'R'-averaged 'offset' SMP-values ≤ − 150 kPa, or equivalently as 'strict' values ≤ − 100 kPa (Appendix 1: Fig. S1). The three 'dry' spells were thus: 18.2.-7.3.2010 (18 days), 12.3 – 28.3.2010 (17), and 11.4 – 28.4.2010 (18). If 'R' values had been corrected according to the w_{40}-predicted regression equations, this threshold would have been lower still after averaging stations; it would have led to slightly different periods being defined as 'dry' on 'R' compared with 'LS'. But differences in SMP between 'dry' and 'wet' are so large, and events developed so rapidly down to values of − 250 kPa and lower, that this was considered unnecessary.

Daily temperature (TEMP) was taken as the mean of logger internal readings at 14:00 h, across the four stations, over the period 6.03.2007 to 4.12.2010. Mean TEMP (with SE) was 26.91 ± 0.04 ºC (*n* = 1370). Over the study period, recordings at the nearby DVFC climate station were incomplete for many variables other than rainfall, but those days with matching values showed dry-bulb temperature at 14:00 h, maximum daily temperature, and number of sunshine hours all to be significantly positively (*r* = 0.734, 0.804 and 0.652; *n´* = 991, 1333 and 786; respectively), and relative humidity at 14:00 h significantly negatively (*r* = −0.658, *n´* = 983), correlated with TEMP. Correlations using only stations 2-4 were very

similar. Plotting graphs showed the relationships all to be linear. TEMP acts as a surrogate for evapotranspiration pull by the trees.

SMP correlated fairly strongly and positively with 10-, 20-, 30-, 40- and 50-day running rainfall totals (both variables sqrt-transformed to achieve linearity), in both wet and dry periods, most strongly with the 10-d value in the wet, and the 20-d one in the dry, period (Table 3). The relationships between SMP and 20-day rainfall totals were adequately described by linear-exponential curves (Appendix 1: Fig. S2). Fits were statistically similar in terms of *F*-ratios for both periods, but the wet with ~ 5.5 times the number of observations of the dry, showed considerably more scatter in SMP (~ 0 to – 120 kPa over the range 100 - 200 mm rainfall totals) than the dry and correspondingly half the R^2-value. SMP was significantly negatively correlated ($P \leq 0.001$) with temperature (logger TEMP; 14:00 dry bulb and maximum daily temperature at DVMC), particularly with the first (Table 3). Temperature variables were also strongly positively correlated among one another in both periods ($P \leq 0.001$).

Diurnal tree girth change was calculated as *per mille* mm with reference to girth at midnight (t = 1), i.e. at 00:00 of the new day, using the formula: $gthch_t = ((girth_t - girth_1)/girth_1)\cdot 10^4$, where t = 1, 2, … 48 for the half-hour times through the day. Whenever a diurnal time series was incomplete, the series of changes was set to ‘missing’ and that day did not count in the finding of means per time of day in a period. The multiplying constant brings the values of relative change into a range of 0 to c. 20.

To test whether daily patterns in girth changes differed significantly in any of the three (17-)18-day dry periods from the longer wet one, the latter was divided into 30 consecutive and similarly long 18-day periods (ignoring the last 10 of the 550 days, and assuming periods to be independent). Mean changes were found per 18-day wet or dry period, and for the wet one the mean of those 30 means and their 99% confidence limits were computed. Should one

or another of the dry-period individual means lie outside these limits, the null hypothesis — that changes in wet and dry are the same— can be rejected at $P < 0.01$. This assumes that no other factors confounded comparisons over time. Variation in mean diurnal SMP for the 30 wet sub-periods and three dry ones (together) was extremely small, only dry 3 showing some downward trend after 10:00 h (Appendix 1: Fig. S3). By contrast, TEMP fluctuated in a clear manner over the day, peaking at ca. 15:00 h, higher in dry than wet periods (Fig. S4).

Means of SMP in the three dry sub-periods were −260, −411 and −290 (together −320) kPa, compared with −36.3 (± 3.7) kPa for the 30 wet sub-periods. These dry sub-periods did not differ significantly in SMP from one another (repeated measures ANOVA, $F = 8.24$, df = 2, 4; $P = 0.097$), nor in topographic location with the plots (lower slope, −354; ridge −287, kPa, P ~ 0.4). The nine-fold difference in SMP between wet and dry periods underwrote the comparison of following tree girth change analyses.

In the following analysis, SMP_0, SMP_{-1}, and SMP_{-2}, and $TEMP_0$, $TEMP_{-1}$, and $TEMP_{-2}$, are respectively SMP, and TEMP, values at no, one- and two-day lags.

Calculations were carried out using Fortran f77 code (FB 6.0, Numerical Algorithms Group, Oxford) to program basic data handling, followed by exploratory analysis and statistical summaries in Minitab (vers. 18, Minitab LLC, Pennsylvania), non-linear regression models in GenStat version 18 (Payne et al. 2011), the time series regressions in R (R_Core_Team 2017), and most of the graphics in `ggplot2` in R (Whickam 2016). Two valuable guiding texts were Venables and Ripley (Venables and Ripley 2002) and Maindonald and Braun (Maindonald and Braun 2010).

Time-series analyses

All trees, minus g13 and g21 were taken with dates ($n = 550$ days) and complete SMP (of four stations) data for the wet period. Numbers of values to be imputed: g14 (12 d), g25 (1

d), g23 (6 d), g22-25 (8 d, 9 d), g32 (3 d), g31-35 (17 d), g41-45 (1 d). These imputed values were set equal to the average of the last and next values. Usually they differed from neither, or from just one by 0.01 cm. In this way a complete set of 550 dates x 18 trees (g11 to g45, minus g13 and g21) was available for autocorrelation analysis. The finding of missing values was achieved in R with the package 'zoo' version 1.8-6 (Zeileis and Grothendieck 2005). Simple wet- and dry-period time series for each girth band are given in Appendix 2: Figs S1 and S2, together with their SMP time series.

For the dry period to be continuously complete as possible several aspects had to be considered. The 6-mo span 01.01 to 30.06.2010 would have been ideal; here station 1 would have been be possible, stations 2 and 3 for 24.02-23.06 only though, and station 4 not at all (because of too many large gaps). By excluding station 4, it was feasible to have 24.02-23.06 as a set 'A', and 18.03-23.06 as a set 'B'. Imputation was as follows: g22-24 (5 d), g31-35 (12 + 2 d), g23 (three scattered single days), so that for set 'A' this meant for stations 2 and 3, 8 and 14 d imputed respectively, and for set 'B' 8 and 2 d. This gave finally a max set 'A' set of 120 dates x 13 trees, and or for set 'B' 103 dates x 13 trees (i.e. as for wet, minus the station 4 trees (Newbery et al.)). To allow sets A and B to be as closely matching as possible, yet make maximal use of the information available, set A was taken from 18.03.2010 to 23.06.2010 (98 d), so-called set A(B) in the archive, and set B 18.03.2010 to 18.06.2010 (93 d). Basic calculations for SMP and girth and their input, merging, matching and checking/evaluation were made in a set of Fortran (f95) programs.

Arima and GLS regression

Mean girth, *gthm* (cm), was found for each day that had complete recordings for the forty-eight 30-min intervals, for each tree in the dry and wet time series. For each day *i*, increments were then found for an interval of 1 day ahead, i.e. $gth_i = (gthm_{i+1} - gthm_i) \cdot 10^3$, i.e. finding the mean *gth* per complete day first, then the increment across days and not the

mean of gth_i-values per day. Corresponding mean SMP-values were transformed as $-1 \cdot (|SMP|)^{1/2}$ and matched to each day's increment.

The dependence of girth increment per tree on SMP in each time series (Appendix 2: Figs S1 and S2) was modelled in two ways: (1) by ARIMA, with SMP as an independent variable, and the parameters p and q fitted either automatically, each allowed to vary up to values of 2, or fixed at either 1 or 2 (Brockwell and Davis 2002, Chatfield 2004), with analysis performed in R using the package 'forecast' (function *auto.arima* | *Xreg*; (Hyndman and Khandakar 2008); and (2) GLS, generalized least squares, regression, where temporal autocorrelation was accounted for with p and q set at either 1 or 2 each (Pinheiro and Bates 2000, Fox 2008), performed with the R package 'nmle' (function *gls* | *corAMRA*; (Fox and Weisberg 2011, Pinheiro et al. 2013). ARIMA and GLS analyses were repeated with SMP lagged by 1 and 2 days.

The values of p and q used in the final GLS models were thus guided by the best fitting ones from ARIMA. Decomposition of the time-series was not possible. Besides there being no clear seasons at Danum, the series were shorter than 1 year (550 and 98 days respectively for the wet and dry periods).

The first 'automatic' ARIMA with the three SMP lags selected p = 1 or 2 (occasionally 3), q = 1 or 2, and d = 1, most often for the best fitting models. By placing restrictions of $p \leq 2$ and $q \leq 2$, very similar results were obtained, and leading to generally lower AIC-values. Differencing was mostly not required (6 or 7 of 18 wet, and 0 or 1, rarely 2, dry bands, had d = 1 selected). Plots of the partial ACF showed that for $p \leq 2$ the functions were often significant ($P < 0.05$), although its ± value declined relatively slowly over higher p-values, indicative of some non-stationarity. Differencing in the form of *gthi*, prior to time-series analysis had the added benefit of making the series more stationary; it also removed net accumulated growth (girth increase) over the time span.

Since the aim of ARIMA here was to find an omnibus for removing autocorrelated variation in the regressions, and not for forecasting, and to a large degree differencing had *de facto* been achieved in the calculation of growth increment, tree-specific settings of d = 1 were not used. Such 'differences in differences (i.e. increments)' would also make physiological interpretations rather obscure. Furthermore, when d = 0 a constant usually (as in R) is estimated by ARIMA. On fitting SMP as the independent variable, this time-series constant would be integrated within the regression intercept term. The value of that final constant is not of prime interest, the focus being response in incremental growth to change in SMP. The p = 2 and q = 2 parameter settings were therefore taken for the *corARMA* function in GLS. It led to just four fitting failures, these due to the coefficients matrix being non-invertibile (Brockwell and Davis 2002): they were remedied by setting p = 3 or q = 1.

Overall, using the same parameterization meant a common model for all trees, across both wet and dry time-series. Adopting q = 2 to reduce the influences of volatility came at the cost of successive growth increments being averaged: a trade-off in increased statistical power versus a dampening of the diurnal response (gth_i). For one tree (g22) a sharp hiatus in recordings (likely caused by falling branch damage to the dendroband) on 27-28.05.2007 meant that only the first part of the wet series could be used. SMP coefficients from GLS with q < 2 were highly correlated with those with q = 2 across species within series indicating strong robustness in the estimations. (For q = 1, wet: 0.993, 0.973 and 0.991; dry: 0.985, 0.971 and 0.983. For q = 0, wet: 0.993, 0.971 and 0.951; dry: 0.987, 0.970 and 0.993, lags 0, 1 and 2 respectively; n_{wet} = 18, n_{dry} = 13, P for all << 0.001). The final GLS regressions with p = 2 and q = 2 were therefore taken as the most robust and realistic set of tests of the influence of SMP on *gthi* adjusted for temporal autocorrelation.

In preliminary runs of time series analysis (not reported here) using growth increments over 2- to 5-day intervals, interpretation was evidently compromised and made very difficult

when q (the moving average term) was ≥ 1. For example, a 3-day increment using q = 0 is a sum, whose average daily equivalent equals the 1-day increment value for the middle day of the three when setting q = 2; this middle day being 1 day advanced with respect to the SMP value (on the first day). Working with growth increments of ≥ 2 days in ARIMA and GLS would necessitate finding mean SMP per increment, which would then lose the diurnal resolution. On these grounds analysis was limited to 1-day growth increment series. In addition, using longer increments led to increasingly higher proportions of model fits giving warnings of statistical conditions being not met in ARIMA, or failing.

GLS regressions were also fitted for gth_i versus TEMP in the same way as for SMP, and then for both terms SMP*TEMP to assess the significance of the interaction. In the latter case only lags of 0 and 1 days were tested.

Since SMP_{-1} was correlated with rainfall totals, *rft* (Table 3), to judge how far the *gthi* regressions on SMP_{-1} might be accounted for by these totals, GLS regressions (p = 2 and q = 2) were run with 10-d-*rft* in the wet period and 20-d-*rft* in the dry (given their improved correlations over 30-d-*rft*). Regressions fitting SMP_{-1} to *gthi* were then repeated with corresponding *rft* terms as the second predictor.

Change in dendrometer band length due to temperature change

The UMS Manual and Data Sheet for the D6 band (UMS, München, Germany) suggest a coefficient of < 1 µm/m/°K for the Invar steel cable and state a 'temperature error' of < 4 µm/°K' for the whole dendrometer. The expansion of the dendrometer is made of two components: (a) the cable itself (λ_1 = 1 µm/m/°K) and (b) the 'block-and-plate' (expansion value unstated by UMS), which together give the < 4 µm/m/°K overall. Since the cables (bands) are of different lengths on the various trees, a correction for each tree's band can be found for them independently. The 'block-and-plate' (which is the same construction for each

band) should, by deduction, account for a < 4 - < 1 = ~ 3 µm/m/°K difference (λ_2). The reader is referred to (Pesonen et al. 2004) and (Wang and Sammis 2008) on the temperature-dependent accuracy of band dendrometers.

Daily temperature differences ($\Delta T = T_{t+1} - T_t$) were found for each tree's band, corresponding to the 1-day increments in *gbh*. When ΔT was positive the dendrometer would have expanded and therefore adjusted the *gthi* should be smaller, and when the ΔT was negative the converse the case. The adjustment was: $gthi_{adj} = gthi - \{((mgbh/100) \cdot \lambda_1 \cdot \Delta T) + (\lambda_2 \cdot \Delta T)\}/k$, where k = 10 is a rescaling factor to convert the adjustment term in µm to $cm \cdot 10^{-3}$ ($m \cdot 10^{-5}$), the unit for *gthi*. GLS regressions (p = 2, q = 2) were rerun using $ghti_{adj}$, for SMP with no lag, and separately for logger-TEMP with no lag, for the trees/bands in the wet and dry periods. Omitting the four trees where volatility was shown, and two very outlying, low, SMP- (slopes < 1.0) and two logger-TEMP-values (slopes < 1.5), regressions for the *n* = 25 species' adjusted versus unadjusted slope-values (estimates for wet {14} and dry {11} periods together) were very strong (R^2 = 99.8 and 99.4% respectively, and these two regression slopes very close to unity {0.978 and 1.015} with intercepts very near zero).

Any errors introduced by expansion or contraction of the bands due to day-to-day temperature changes were therefore very small and could be neglected, and certainly very minor compared with differences between trees. Accordingly, the analyses presented for SMP and temperature effects on gthi are presented without adjustment. The two outliers were also close to the lines for the 25 points but afforded high leverages).

Could diurnal changes in the bands have been in part due to daily temperature change? From the DVMC climate station, dry-bulb temperatures at 08:00 and 14:00 h in the wet period were 24.3 and 30.0 °C on average, and in the dry period correspondingly 25.3 and 31.7 °C; ΔT being then 5.7 and 6.4 °C for wet and dry periods. Although there are no records for temperatures at DVMC at midnight, Appendix 1: Fig. S4 shows for example that minimums

were usually around 08:00 h. However, the *gthch* variable was calculated with 00:00 h as reference, and the mean logger temperatures at this time (t = 1) and the maximum at station 1 were 23.5 and 26.5 ^{o}C in the wet, and 24.6 and 28.7 ^{o}C in the dry, period; ΔT being 3.0 and 4.1 ^{o}C for the two periods. Logger temperatures at 00:00 h were 1.0 to 1.1 ^{o}C higher that those at 08:00 h. In the daytime the temperature sensor would, furthermore, have been somewhat insulated, from especially the higher temperature extremes, within the logger housing. The temperature curves for the other three stations were very similar. Taken together an average upper maximum diurnal ΔT experienced by the bands can be estimated at ~5.5 ^{o} C. Applying this in the formula for band expansion given above, a tree of 30 cm *gbh* would have maximally expanded 0.62 *gthch* units, and one of 100 cm *gbh* by 0.22 (the change being relative to *gbh* at $t_{1;}$ most of the expansion in the 'block-and-plate'). These are very small values when judged against diurnal band fluctuations. Temperature change therefore affected the species' diurnal *gthch* patterns very minimally, at least as far as the bands themselves were concerned.

A coda is required here. No correction or allowance was made for possible thermal expansion of stem wood. This is likely to have been of the same order of magnitude as the bands (Sevanto et al. 2005) but estimation of the necessary parameters for the six Danum tree species was not feasible during the present study.

Non-stationarity

After fitting auto-arima models (Xreg = SMP) with lags in SMP of 0, 1 or 2 days, the ACFs of the squared residuals were examined for evidence of non-stationarity of variances, and any departures fitted using GARCH models (Enders 2015). These calculations were made with R package 'tseries' (function *garch*). In testing at $P < 0.05$, emphasis was placed on ACF for p = 1 to 3, and whether ACFs (ε^2) were $P << 0.05$ significant. Occasional small divergences at p = 1 to 3 were counted as weakly non-significant. For SMP lag = 0 (and 1 and

2), three of the 18 'wet' bands (viz. g14, g23 and g41) showed obvious and strong heteroscedacity (Appendix 2), removable with GARCH model fits (p = 1, q = 1) for bands g14 and g41 but not band g23 (with any p = 1 to 3). Band g22 had an isolated very high variance episode early in the time-series (Appendix 2: Fig. S1) and this was clearly highlighted by the ACFs (ε^2) and GARCH.

Using SMP lags 0, 1 and 2, for a second test of non-stationarity, the wet series of 18 bands were each divided into three parts. For the four bands where ACFs (ε^2) indicated non-stationarity (heteroscedacity), were divided unequally so as to have a 'normal' subseries, then a volatile part, and finally a return to 'normality'. For the other 14 bands the series was divided into equal parts. `Auto.arima` (max.p = 2, max.q = 2) and `gls` (p = 2, q = 2) were run for each band, and estimated SMP coefficients for subseries plotted against one another. (In three of 54 cases it was necessary to reset q to 1 to obtain a solution.) The coefficients from arima and GLS generally matched very well for each subseries, but not always well *between* them (within series). Of the four 'suspected' series, g14 and g22 certainly behaved differently in the middle periods (i.e. not only was variance higher but slope different), whilst for g23 and g41 there was scarcely a difference (i.e. despite the raised variance, slopes remained similar). For g14 and g22, coefficients were respectively much more positive and negative than the low variance subseries before and after.

To summarize, the tree/species *gth* vs SMP relationships with minimum effect of volatility, GLS coefficients for g14, g23 and g41 bands were averaged for their first and third subseries, and combined SEs found as the root mean squares (geom. means) of the two subseries' values. Likewise, the two *t*-values were averaged and a new $P(t)$ found (with {550/3}-2 = 181.3 df). For band g22, the first 100 days of the wet series were omitted because, beside the extreme volatility early on, there was the above-mentioned unusual down-shift in *gth* in May 2007; and thus its GLS was based on a third subseries of 450 days. The

four bands' new estimates replaced the full series ones, giving a more robust and conservative time-series regression model fits for them.

For comparisons across trees and species, and in relation to other variables, SMP_{-1} and $TEMP_0$ coefficients from the time-series GLS fitting were girth-standardized through multiplication by 50.0/*gbh* (in cm).

Granger causality

Granger causality testing provides an omnibus method for detecting whether for two time-series variables, Y_t depends on X_t when both are included in an auto-regressive model, each with increasing lags in *t* up to *p* (Granger 1969). A significant *F*-ratio indicates whether a least one X_t term is determining at least one Y_t term. The test was implemented with `grangertest` in R package `lmtest`, for *gthi* as Y and either SMP_0 or $TEMP_0$ as X, for the wet and dry periods separately. By setting $p = 2$, SMP_{-1}, SMP_{-2}, $TEMP_{-1}$ and $TEMP_{-2}$ were included in the model.

RESULTS

Diurnal variation

All 18 trees allowed a comparison in daily *gthch* between wet and dry periods, expressed on a per mille (‰) basis and referenced to zero-midnight. The 30 sub-periods showed a repeatable and consistent pattern, a rise in *gthch* in the early afternoon. The peak was barely detectable for large trees over 60 cm *gbh*, particularly the dipterocarps; was moderate for the understorey species *D. muricatus* (`Dm`), *L. beccarianum* (`Lb`) and *M. wrayi* (`Mw`), but most pronounced for the small dipterocarps (Fig. 3). In the dry period compared with the wet one, again the large dipterocarps showed only small increases (outside of the wet

period confidence limits), suggesting that they were little affected by the drier conditions. The understorey species, though, showed a mix of response curves with generally a dip in *gthch* late morning (especially for *M. wrayi*), and then an overshoot in late afternoon. By contrast to *M. wrayi*, *D. muricatus* showed little response (Fig. 3). Interesting, among the large-treed species, *P. malaanonan* (Pm) tended in its behaviour towards the understorey ones. Largest responses diurnally were again for the small trees of the overstorey dipterocarps, very clearly for two of these three *S. fallax* (Sf) trees, one with a late-morning dip like *M. wrayi*. The two trees of *S. parvifolia* (Sp) behaved differently in the dry period but not markedly so. Small dipterocarps appeared therefore to benefit from the dry period, the understorey species little. Presumably the climate was not severe enough for water availability to limit growth and evapotranspiration, and the increased light in the understorey was utilized best by the shade-intolerant small trees of the overstorey species. Among the 12 small trees (*scl* = 1, Table 2), the four species did not differ significantly in their mean minimum or maximum diurnal *gthch*-values (P = 0.08 – 0.65; analysis of variance, with stations as randomized 'block' term).

Changes over longer time in relation to soil moisture and temperature

The growth increment between the current day (gth_i) and the next (gth_{i+1}) was regressed against the current day's mean soil moisture potential (SMP_0), that of the day before (SMP_{-1}) and of two days before (SMP_{-2}). To recall, three bands' series in the wet period were adjusted for non-stationarity. Bonferroni correction to the P-values for the regression t-values was applied in a rudimentary way, by simply dividing the critical α by 18 and 13 for the wet and dry periods' samples of trees respectively and quite conservatively guarding against type I errors due to multiple testing.

Of the 18 wet period trees, gth_i was significantly related to SMP_0 for eight of them (6 negative, 2 positive), but with many more for SMP_{-1}, with 14 trees (8 negative, 6 positive),

and then with 11 trees for SMP_{-2} (6 negative, 5 positive) (Fig. 4; Appendix 3: Table S1). For most trees the most significance attached to the slopes was for SMP_{-1}, sometimes similarly strong for SMP_0. In all but two cases the direction was the same across SMP_0 to SMP_{-2}, and in those opposite cases the change was with insignificant slopes using SMP_0. For the 13 trees in the dry period, just one was significant (positive) for SMP_0, five for SMP_{-1} (three positive, two negative), and then just two for SMP_{-2} (both positive). Two conclusions follow. The dependence of gth_i on SMP was strongest (i.e. most significant) largely with the soil potential of the previous day (SMP_{-1}), and the significance in the wet period much higher than in the dry one. Significance will depend in part on sample sizes: the wet had more time points than the dry period (Appendix 1: Table S1).

Girth increment dependence on temperature was similarly analyzed using current logger temperature ($TEMP_0$), and the lagged values $TEMP_{-1}$ and $TEMP_{-2}$. It was clear that most significance was reached with $TEMP_0$, with 13 slopes (12 positive, 1 negative), yet $TEMP_{-1}$ had only four cases (all positive), and $TEMP_{-2}$, just two (one each positive and negative) (Fig. 5; Appendix 3: Table S2). Interestingly, for at least those significant the relationship was with opposite slope using $TEMP_{-1}$ than it was using $TEMP_0$. For the dry period, three trees only were significantly related to $TEMP_0$, and four with $TEMP_{-1}$ (all negative), and just one being negative for $TEMP_{-2}$. Switching of slope direction was less consistent in the dry than wet period. Hence, the most significant effects were concentrated on $TEMP_0$, with little lag effects apparent, and again more cases significant for wet than dry period (Appendix 1: Table S1).

The two-term regressions support the one-term ones (Appendix 3: Table S3 and Appendix 4) with the most significant slopes being for SMP_{-1} and $TEMP_0$, with SMP_{-1} and $TEMP_{-1}$ closely second. The *t*-values for the coefficients were strongly correlated across columns in Table S3 especially when SMP_{-1} was involved. Dry period significances were

often not high, although more often so for SMP_{-1} and $TEMP_0$. The slopes for temperature in the two-term regressions showed a more significant outcome when potential was SMP_0 or SMP_{-1}, but the temperature $TEMP_0$ (Appendix3: Table S4 and Appendix 4). Agreement across the columns was very high, and for the dry period more slopes were significant than in the one-term regressions (six each) for $SMP_0/TEMP_0$ and $SMP_{-1}/TEMP_0$. Unsurprisingly, from these last results, the tests of significance for SMP*TEMP interactions were almost completely non-significant, except for two isolated cases (Appendix 3: Table S5). Hence, the two-term regressions affirmed the one-term ones, with SMP-1 and TEMP0 being most important and them not having interactions. This implies that SMP and TEMP were acting independently.

The sizes of the regression coefficients in the wet and dry periods do not necessarily match the relative sizes of the *t*-values since the dry had larger SEs than the wet period. Guided by the most significant outcomes from the regressions, i.e. focusing on those that used SMP_{-1} and $TEMP_0$, wet and dry period slopes may be compared for each tree in Figure 4 in turn. Starting with SMP_{-1} (centre bars of each panel), the majority showed similarly positive or respective negative values across the two periods. The two exceptions in Figure 4 are g12 and g33 (marginally also g35). Although the effects were strongest for lag of 1 day they were not absent for lags 0 and 2 days. The ± 1 SE bars give an approximate indication of strengths of differences between periods, but since the same tree is considered in both periods wet and dry period data are not statistically fully independent even though within period temporal autocorrelation was accounted for by arima. Twelve of 13 trees had wet and dry period slopes in the same direction for SMP_{-1} (i.e. both positive or both negative) (Fig. 4) and g32 was not following the rule. For seven trees the wet slope value was larger than the corresponding dry one, and in six cases the converse. In summary, there was no overall common differential response to period. For g12, g22, g25 and g35 (possibly also g34) was the difference towards

significance. The slopes for SMP0 and SMP_{-2} showed less strong differences between the periods than did SMP_{-1}. These relative SMP_{-1} slope values will be returned to later. The five trees at station 4, which lacked dry period estimates, showed consistent slope values for SMP_0 to SMP_{-2}.

Taking the values of $TEMP_0$ slopes (left bars in the panels of Fig. 5) for reference, lags and wet-dry differences in mean gth_i can be compared too for response to temperature. Compared with SMP, there are many more switches in slope directions between $TEMP_0$ and $TEMP_{-1}$ and $TEMP_{-2}$. Values that were often positive for both wet and dry periods became negative; occasionally, this was in the opposite way (for g12 and g33). Differences between wet and dry period slopes were also quite variable. For g15, g22, g24, g25 and g35 they were similar, but for the other bands they showed slopes for wet > dry period (Fig. 5). Switching from positive to negative between periods was obvious for g11, g23, g33 and g34, and negative to positive (g14). The SEs on TEMP coefficients were similar to those for SMP but rarely was there a tendency towards possible significance in period differences. Furthermore, and again in contrast to responses to SMP, the five trees at station 2 showed much more variable slopes for $TEMP_0$ to $TEMP_{-2}$, even two switching direction (g42, g43).

Graphing the mean coefficients for gth_i depending on SMP, and on TEMP, from the two-term regressions in a factorial SMP_0-SMP_{-1} x $TEMP_0$-$TEMP_{-1}$ arrangement for each tree (Appendix 3: Figs S1 and S2), illustrated a high degree of correspondence across the four combinations of the variables. With the focus still on $SMP_{-1}/TEMP_0$, the key bars are the second and third sets (paired wet and dry) in Figs S1 and S2 respectively. Notable deviations occurred for g25, g33, g35 and g42 for SMP coefficients, and marginally just g35 and g44 for the TEMP ones. Nevertheless, analysis of variance for *scl* = 1 trees (run in the same way as for *gthch*) showed no significant differences (P = 0.20 - 0.79) in the two variables in either

period. These comparisons give support to concentrating on comparing tree sizes and species identities between wet and dry periods for essentially $SMP_{-1}/TEMP_0$.

Under the Granger causality test, SMP was highly significant for many more trees than was TEMP in the wet period (*F*-values for $p = 2$ in Appendix 1: Table S2): 16 and 14 cases at $P \leq 0.05$ and $P \leq 0.001$; and correspondingly 6 and 5 cases at these levels, respectively. In the dry period significant effects were fewer and similar for the two variables: 6 and 3 for SMP and 5 and 2 for TEMP. On this basis, SMP would appear the stronger cause of *gthi* than TEMP. For the 18 wet and 13 dry period bands, plotting the Granger's *F*-values against the *t*-value for the corresponding GLS coefficient squared ($n = 31$) resulted in rather low correlations ($r = 0.406$, $P = 0.024$; and $r = 0.248$, $P = 0.19$; for SMP and TEMP). The test was probably finding best fits with lags in the X-variable where occasionally for some trees SMP_{-1} and $TEMP_0$ were not the best fitting ones individually in the GLS models when compared with the alternatives.

Variation in girth increment with tree size

Girth increment, *gthi*, varied widely across the banded trees in both wet and dry periods in terms of means and standard deviations (Table 4). The quantiles indicated that positive and negative values were roughly equally distributed in the wet period, but in the dry one they were more positively skewed. Although *gbh* was a major factor in determining *gthi*, there was still considerable variation in mean and SD of *gthi* among the small trees (*scl* = 1; Fig. 6). Mean and SD of *gthi* were positively correlated in the wet period ($r = 0.482$, $P \leq 0.05$, df = 16) but not significantly correlated in the dry one ($r = -0.272$, $P = 0.37$, df = 11). Large trees (in the overstorey) are well separated from the small ones (in the understorey) in Fig. 6. When just the small ones are considered, these form a cluster with mean *gthi* close to zero in the wet period (Fig. 6a) but with much more variation in SD of *gthi* (Fig. 6c). Contrastingly, in the dry period the spread in mean *gthi* was quite obvious (Fig. 6b) and the corresponding

SD values even more so (Fig. 6d). Differences and variation in responses among trees were more marked in the dry than wet period. As expected, simple-difference absolute growth rates (*agr*, mm/year) of the banded trees over wet and dry periods were almost perfectly linearly related to mean *gthi* (slight variation due to shrinking/swelling on the first and last date of period): agr_W = -0.09 + 3.64 $gthi_{mn}$ for the wet, and agr_D = 0.25 + 3.78 $gthi_{mn}$. The difference in intercept from zero in the dry period reflects the negative skew in the *gthi* values.

Absolute values of the coefficient of variation (sd/mean) *gthi* were generally higher in the wet (1.5 – 375) than dry (1 – 25) period, for the 13 trees recorded in both (Table 4). This implies that the contribution of growth to *gthi* compared with water-flux related fluctuations not only varied very considerably (relatively much when the ratio was low, conversely little when it was high), but more so in the dry than wet even though the dry created larger fluctuations. Across these 13 trees however, mean mean-*gthi* (and SE) were 1.47 ± 0.82 and 1.20 ± 0.54 cm·10^3 in the wet and dry periods respectively. Based on this limited sample, growth rates overall barely differed between periods. The results highlight again the considerable variability between individuals in their growth rates and responses.

SMP and rainfall

Since *n*-d rainfall totals were positively correlated with SMP_{-1} (Table 3, variables sqrt-transformed), using both as predictors in a regression may have involved some collinearity. Cross-correlations of estimates of the SMP_{-1} coefficients from regressions of *gthi* on SMP_{-1} alone (the original model) and those from now regressions of *gthi* on SMP_{-1} and *rft* (using the 10-d and 20-d values for wet and dry periods respectively), were r = 0.406 (P = 0.095, df = 16) in the wet, and r = 0.661 (P = 0.014, df = 11) in the dry, period. Their corresponding *t*-values were better correlated (r = 0.771 and 0.671, P < 0.001 and 0.012). Using the residuals from a first linear regression of SMP_{-1} on *rft* led to almost identical coefficients and *t*-values.

In the wet period slopes of *gthi* on 10-d-*rft* were significant for just one band, g31 ($P < 0.01$, $\alpha' = \alpha/18$), and in the dry period the same on 20-d-*rft* for two bands g32 and g34 ($P < 0.05$, $\alpha' = \alpha/13$ resp.). Comparing SMP_{-1} estimates from gls model fits with and without the corresponding wet- or dry-period *rft*-term, now omitting the four bands which showed volatility and needed GARCH adjustments, the relationship became approximately linear especially when the estimates were both negative (Appendix 1: Fig. S5). However, where the single-term model estimate of SMP_{-1} was positive, that from the two-term model deviated considerably from the line, more so in the wet than dry period (Fig. S5). Band g12 might qualify as an outlier in Fig. S5a; and it was noted before as having unusual lag patterns in the wet period (Fig. 4). Bands g12 and g33 had likewise unusual patterns in the dry period. Leaving aside these unusual bands, concave curves fit the points quite well (Fig. S5c, d). When *rft* was included in the gls models, slopes of regression of *gthi* on SMP_{-1} that were negative in the single-term gls fit became more negative, and those that were positive, more positive. The gradient where the estimate of SMP_{-1} in the single-term model was equal to 0 was 4.286 in the wet, and 3.352 in the dry, period.

Relationships between coefficients and descriptor variables

Standardized SMP_{-1} and $TEMP_0$ coefficients were positively and strongly significantly correlated in the wet period ($r = 0.811$, $P \leq 0.001$, df = 16) and it is clear from Fig. 7a that small trees (*scl* = 1) had mostly positive, and large trees (*scl* = 2) all had negative SMP_{-1} values. In the dry period the relationship was weaker and non-significant ($r = 0.341$, $P = 0.25$, df = 11), but then the three large trees were occurring near the centre, in among the small-tree SMP_{-1} and $TEMP_0$ values (Fig. 7b). Considering just the small trees (*scl* = 1), in the wet period the correlation between SMP_{-1} and $TEMP_0$ was very similar and significant to using all trees ($r = 0.810$, $P = 0.001$, df = 10), yet no better in the dry period ($r = 0.365$, $P = 0.30$, df = 8). SMP_{-1}-dry and SMP_{-1}-wet were positively correlated ($r = 0.741$, $P \leq 0.01$, df =

11; Fig. 7c) but this was not the case for $TEMP_0$-dry and $TEMP_0$-wet (r = 0.263, P = 0.39, df = 11; Fig. 7d). Again, taking just the small trees these last two relationships became respectively more and less significant (r = 0.936, $P \leq 0.001$, df = 8; r = 0.149, P = 0.68, df = 8). The correlations between SMP_{-1} and $TEMP_0$ involved species that were each represented by two to four trees, so there may have been some phylogenetic effect in trait terms, points for the same species being not fully independent of one another. However, the replicate trees within species were well-dispersed so any effect would have been very small.

Canopy status, CanStat, was strongly and significantly positively correlated with *gbh* (r = 0.917, P < 0.001, df = 16; CanStat = 1.426 + 0.02761 *gbh*), and on the basis of trees divided into the two *scl* classes (under- and overstorey), the ~ 60 cm *gbh* threshold was equivalent to a CanStat value of 3.08. Canopy status is used further here, rather than *gbh* per se, because as a composite measure this first variable probably reflects much better the light levels directly above crowns and, therefore, indirectly the evapotranspiration as radiation and thus temperature changed. CanStat was strongly positively correlated with absolute stem growth rate in the third main-plot census period P3 (2001-2007), agr_{P3} (r = 0.668, P = 0.002) but less well with the corresponding relative stem growth rate, rgr_{P3} (r = 0.400, P = 0.10).

SMP_{-1} was strongly negatively correlated with CanStat in the wet period (r = −0.687, P < 0.002, df = 16), but not in the dry one (r = −0.116, P = 0.71, df = 10) (Fig. 8 a, b). For $TEMP_0$ in the wet and dry periods correlations were similar (r = −0.627, $P \leq 0.01$; and r = −0.221, P = 0.49 respectively; Fig. 8 c, d). For small trees only, SMP_{-1} was again correlated negatively with CanStat in the wet period (r = −0.531, $P \leq 0.10$, df = 10), and also in the dry one (r = −0.520, $P \leq 0.12$, df = 8); and it was so for $TEMP_0$ in the wet (r = −0.608, $P \leq 0.05$, df = 10) but not in the dry (r = −0.133, P = 0.71, df = 8). It is interesting that the strong negative correlation of SMP_{-1} and $TEMP_0$ with CanStat, occurring in the wet but *not* dry period for all trees, was shown again especially for SMP_{-1} in the dry period for small trees.

Neither the adjusted coefficients of SMP_{-1} nor of $TEMP_0$ in the wet and dry periods differed significantly between stations (F = 0.46 to 1.49, df = 3,14 or 2,10; $P > 0.25$), although mean SMP_{-1} coefficient did decline the most from 1.05, 0.64, −0.05 down to −0.56 between stations 1 to 4 in the wet period (Appendix 1: Fig. S6). In the corresponding dry period mean SMP_{-1} coefficients were 0.38, 0.33, and −0.48 across stations 1 and 3. There was therefore some tendency for SMP coefficients to be more negative on the ridge (3 and 4) than the lower slope stations (1 and 2), which might indicate stronger competition for water on ridges than lower slopes.

Relationships between coefficients and diurnal changes

The average minimum and maximum *gthch* (Fig. 3), in the wet and dry periods, might represent a trait underlying species' responses to water stress, i.e. a physical-physiological capacity to increase or decrease *gth* as water flux changed in the tree. Trees with large ranges or 'flexibility' might be seen as being more responsive than those with small ranges. The more responsive species would be expected ex hypothesis to have more pronounced SMP_{-1} and $TEMP_0$ time-series coefficients than less responsive ones.

A surprisingly large variability, not only with respect to tree size (*gbh*, *CanStat*, or *scl*) but also within-species — even where tree sizes were similar, is shown in the relationships between the two time-series coefficients and *gthch* statistics (Figs 9 and 10). Since 'replicate' trees were scattered widely across the panels of these figures, phylogenetic influence is likely to be very low, and a high level of tree individuality is indicated. Correlations were positive and significant for SMP_{-1} (r = 0.523, $P \leq 0.05$; Fig. 9a) and $TEMP_0$ (r = 0.735, $P \leq 0.001$; Fig. 9c) versus $gthch_{min}$ in the wet period; likewise, for SMP_{-1} (r = 0.640, $P \leq 0.01$; Fig. 9b) and $TEMP_0$ (r = 0.658, $P \leq 0.01$; Fig. 9d) versus $gthch_{max}$, though notably the three trees of *S. fallax* were the most outlying graph points. In the dry period the correlation for SMP_{-1} versus $gthch_{min}$ was stronger (r = 0.609, $P \leq 0.05$; Fig. 10a), yet for $TEMP_0$ versus $gthch_{min}$ it was

lost ($r = -0.284$, $P = 0.35$; Fig. 10c). An even stronger positive correlation for SMP_{-1} versus $gthch_{max}$ ($r = 0.703$, $P \leq 0.01$; Fig. 10b) was due in part to the positively skewed values for the two small trees of *S. fallax,* and similarly was the case for $TEMP_0$ versus $gthch_{max}$ ($r = 0.570$, $P \leq 0.05$; Fig. 10d). Considering just small trees (*scl* = 1), correlations with $gthch_{min}$ and $gthch_{max}$ were all positive but non-significant in the wet period ($r = 0.455$ to 0.538, $P > 0.07$). They did remain significant in the dry period for SMP_{-1} ($r = 0.661$ and 0.753 respectively, $P \leq 0.05$) though not for $TEMP_0$ (r = −0.234 and 0.549, $P > 0.10$). In Figs 9 and 10, replicate trees of species of the same species were not closely positioned to one another in either period, the species being well mixed within panels.

Average SMP_{-1} coefficients decreased between the wet and dry periods, twice as much for *D. muricatus* as for *M. wrayi* (Table 5). Those for $TEMP_0$ decreased even more for *D. muricatus* though hardly at all for *M. wrayi*. For both variables the replication at the tree level is too low for formal tests of significance, although bearing in mind the significance of each estimated coefficient, there is an interesting indication that *D. muricatus* was more resistance to the drying than *M. wrayi*. One difficulty was that among the three to four trees of these two species there was one in each case each that behaved quite differently from the others.

Influence of local tree basal area abundance

For each of the 12 understorey (*scl* = 1) trees, one measure of neighbourhood competition is the sum of basal areas (*BA*) of either all trees ≥ 10 cm *gbh*, or those with greater *gbh* than the focus tree considered, within a 5-, 10-, 15- or 20-m radius (*d*) and with each tree inversely weighted by its distance to the focus (*BA/d*). Relevant data of the 2007 census in the main plots at Danum were abstracted from calculations made for a recent tree survival analysis (Newbery and Ridsdale 2016). Coefficients of SMP_{-1} and $TEMP_0$, in neither the wet nor dry periods, were significantly correlated with any of the eight neighbourhood values ($P = 0.11$-0.96). At 5-m radius all trees made *BA/d* =167-2684 cm^2/m (two high

outliers of *D. muricatus* and *S. fallax* (Dm4,g42;Sf3,g25) of 1286 and the maximum cm^2/m); and at 10-m radius the corresponding range in *BA/d* was 593-3442 cm^2/m. There were no clues to help explain differences in SMP_{-1} and $TEMP_0$ coefficient values, and the separation of points for trees within species in Figs 6-9. The expectation was that small trees with large neighbour *BA/d*-values would have suffered more from competition for water, especially in the dry period, than those with small values: but this was clearly not so from the evidence. Three of the 12 banded trees were small representatives of the overstorey species *S. fallax* (Sf). They had no conspecific larger (Sf) neighbours with 10 m radius, and just one of them (Sf4, g41) had one medium-sized tree positioned between 10 and 15 m: thus, no evidence for a conspecific effect either. The wet period was close to this 2007 census and thus the BA/d values apply: but by the time of the dry period in 2010 neighbourhood could well have changed due to tree deaths occurring. Between 2007 and 2015, ten trees with *gbh* ≥ 100 cm died in the 20-m neighbourhoods of the eDDs trees: 0, 3, 3 and 4 in stations 1 to 4 respectively. However, the corresponding numbers of trees with volatile time-series at the stations were 1, 2, 0 and 1 (of the 18 in total), showing very little association with local tree death at all. The precise dates on which these trees died within the period is unknown.

Relative values of SMP_{-1} and $TEMP_0$ coefficients, in wet and dry periods, for small trees of the same species (Table 2) were compared with respect to their *BA/d* at 5 and 10 m radius. In no case for the four species could a consistent ranking be found. This would suggest that any adjusting effects of *BA/d* on *gthi* dependence on these variables (indicating perhaps local competition for water) were absent, and there must be other explanations for within-species variation. There was no correspondence between individual tree SMP_{-1} coefficients for *D. muricatus* and *M. wrayi* and their local *BA/d* values.

DISCUSSION

Large and small trees

The relationships from the temporal-autocorrelated adjusted time-series, were summarized in the slopes or coefficients of *gthi* on either SMP_{-1} and $TEMP_0$. *Gthi* was a forward variable (i −> i+1), and SMP_{-1} and $TEMP_0$ were backward ones (i−1 and i respectively). $TEMP_0$ was an external variable to the trees, unaffected by their water fluxes (unless evapotranspiration was also cooling the forest), so it could be considered a cause of *gthi*, because it largely preceded *gthi* (there was approximately half of a day of overlap). Although logger temperature was recorded inside the forest, it correlated well with external temperature at DVMC. SMP_{-1} was only in part an external variable though, because it was determined by both rain fall into the top 20 cm of soil (expressed as a total over the *n* preceding days), and by the uptake of water driven by evapotranspiration in the canopy (i.e. by $TEMP_0$). SMP_{-1} was averaged across the four stations, that is it was a variable common to plot and forest (as was $TEMP_0$). On hot sunny days (with high $TEMP_0$) strong transpiration pull will have acted on all trees, those being recorded *and* their neighbours. Each tree's response would have been in part also influenced by trees in its own neighbourhood, but the data set does not allow an analysis at that level of SMP spatial resolution. Soil sensors in any case were not placed exactly close to particular banded trees, but distributed among them at random. SMP_{-1} was therefore a potential cause of *gthi*, but at the same time it was also determined by it when water flux was being driven by evapotranspiration.

It was SMP_{-1}, and not SMP_0, that was mostly the better predictor of *gthi*. $TEMP_0$ could not have been a direct cause of SMP_{-1} since that would have implied causality acting in a backwards manner. It is possible though that $TEMP_{-1}$, and even $TEMP_{-2}$, being temporarily correlated with $TEMP_0$, were acting on SMP_{-1}, although their effects were not so strongly as indicated by the two-term GLS model fits. It appears further that SMP_{-1} and $TEMP_0$ were

acting fairly independently and were therefore additive. SMP largely affected *gthi* the day before TEMP did. From this it must be concluded that had TEMP (i.e. evapotranspiration), and/or *gthi*, any indirect effect on SMP_{-1} this would have been prior (at a negative lag) to the direct effect of SMP_{-1} on *gthi*. A simple interpretation is that rainfall (positively) and evapotranspiration (negatively) together determined SMP_{-1}.

In the wet period, large trees had notably the strongest negative SMP_{-1} coefficients, and these were similarly strong for SMP_0, SMP_{-1}, and SMP_{-2}. The smaller trees were not only much more mixed in sign of the coefficients but also much more variable across the lags in SMP. Likewise, for TEMP the large trees had almost always positive coefficients in the wet period, especially for $TEMP_0$ but more weakly for $TEMP_{-1}$ and $TEMP_{-2}$. These large trees were driving the evapotranspiration of the forest through water uptake, which was lowering SMP for all trees, large and small. It was unfortunate that four of the six large trees lacked dry period SMP data (station 4). It is tentatively assumed that they would have responded like g12 and g22 to also have *gthi* reduced close to zero in the dry period. In the wet period, g12 behaved rather differently from the other five large trees, however. Large trees were affecting the SMP in the soil much more, also responding differently between periods, than small ones. Smaller understorey trees were mostly well shaded (i.e. low CanStat) so their demands for water use were less than those of the canopy trees.

Feedback and response

The aim of the present paper was not to advance mechanistic tree water relations models at the detailed level of (Mencuccini et al. 2013), (Steppe et al. 2006, Steppe et al. 2008) or (Zweifel et al. 2005), because complete series of climate variables were unavailable for Danum. Ideally radiation could have been used to estimate potential evapotranspiration. SMP was measured only in the top soil profile layer, and TEMP as ambient (logger) temperature. The data are then best used at the system level, in a phenomenological way,

when asking whether different species had characteristically different responses that were possibly indicative of any water-use traits. Hidden within the daily mean changes in girth will have also been hysteresis (Garnier and Berger 1986, Simonneau et al. 1993), an asymmetric relationship between *gthi* and soil moisture potential, picked up as part of the diurnal patterns. Furthermore, to separate short-interval growth increments from water-flux-induced stem changes (as done by (Zweifel et al. 2001, Zweifel et al. 2005) would have been very difficult from visual inspection of the *gthi* time-series (Appendix 2). There were rarely any clear 'ledges' over several days below which *gth* could be inferred to dip due to shrinkages, followed by an unambiguous 'step-up' in increment that could be attributable to intrinsic growth (see (Zweifel 2016). Each increment (*gthi*) was part swelling-shrinkage, due to changes in rates of water flux, and part growth, even when *gthi* was negative, in either wet or dry periods. Most trees did have net positive changes over the entireties of the two periods which indicated net absolute growth.

An aspect of systems analysis is how feedback is expressed within a time-series: each day's response as *gthi* will have depended on responses the day before, the system (tree) state, and the environmental conditions before and on the day considered. Evapotranspiration output, represented by TEMP, used the water supplied via the vascular network, and created a decrease in SMP which was balanced over time by an increase in potential as a result of rainfall input. Different species may have been more or less sensitive to decreases in SMP_{-1} (or what it represents) conditional on their different evapotranspiration demands. What was happening diurnally provided a set of averaged 'reference pictures' of the trees' rhythms. The patterns became modified from day to day as SMP_{-1} and $TEMP_0$ changed. A central question was whether different types of diurnal pattern related to the different forms of response described by the time-series regression coefficients.

How would different groups of understorey species have been expected 'hypothetically' to respond in a forest free of neighbours with varying influences (a common neighbourhood)? All species would have responded positively to increased $TEMP_0$ (more radiation, more photosynthesis, more water usage and flux) but differently when water became limiting. For a small tree of the drought-tolerant understorey guild transiting from wet to dry period this might have led the positive dependence of *gthi* on SMP_{-1} to become less steep or close to zero. Being able to tolerate the lowest SMP_{-1} levels *gthi* was little affected, although possibly at the cost that there was no advantage when SMP_{-1} was high (under a form of ecophysiological trade-off operating). Conversely, a non-tolerant understorey species would probably have had a steeper coefficient than average, more affected when SMP_{-1} became very low yet not necessarily responding better when relieved of the stress. Drought-intolerant small trees of overstorey species would have been expected to reduce *gthi* at very low SMP_{-1} but responding appreciably better when SMP_{-1} was near zero. Additionally, there is perhaps a fourth guild, not obviously represented in the data set, composed of small trees of overstorey species that were more tolerant of drought (e.g. *Parashorea*). These trees would have been less affected by SMP_{-1} and responded to its increase at a slower rate than the intolerant species, again involving a possible trade-off.

Understanding how the internal cycle within the tree, expressed as response in *gthi*, was affected over time by the two external factors rainfall and TEMP, requires a recognition of reciprocal feedback control between TEMP (as proxy for evapotranspiration) and SMP. This was postulated to differ between wet and dry periods. It requires examining whether the time-series regression coefficients were positive or negative – and how significantly, and whether they accorded with the physics of tree-water relations for different forest structural guilds. When SMP declined its values became more negative: when TEMP declined it became less positive. Large overstorey trees are generally expected to exert much greater

transpiration pull on the soil water than smaller understorey ones due to their larger biomasses. It is important here to re-emphasize that SMP_{-1} and $TEMP_0$ had coefficients in almost all cases of the same sign as, but stronger (and usually more significant) than, the alternative lags considered, viz. SMP_0 and SMP_{-2}, and $TEMP_{-1}$ and $TEMP_{-2}$. This is not to say that those latter variables were not acting at all. But, if these other variables were causing, even in part, *gthi* variation, it is inferred that they were doing so more weakly than the two most-significant ones highlighted. There were a few unexplained exceptions, however (Figs 4 and 5).

Grainger testing was not too informative because it could not test specific hypotheses about where the defining time interval between cause and effect was essential. On the other hand, it picked up significant causal effects among the lagged X-terms (SMP_0, SMP_{-1} or SMP_{-2}) and hence trees where SMP_{-1} was not the only best correlate. Granger-causation testing furthermore assumes unidirectional causality and does not guarantee that only 'X caused Y' — any more than GLS regression does, because both variables may have been driven by a third variable Z; X and Y were merely correlated (Eichler 2013). (Cartwright 2007) and (Kleinberg 2013) provide interesting discussions on the detection of causality from time-series data, and on the limitations of Granger's approach. An important lack in the Danum stem girth data was not knowing all the other variables that influenced a focal tree's SMP_{-1} and its *gthi*. Two such factors, highlighted above, were (1) how SMP changed with rooting depth, and (2) the influences of neighbour trees' water uptake, and their <u>own</u> SMP_{-1}-*gthi* relationships. Without having hierarchically nested models the method could not point to *which* lag in X was most important for predicting Y. Temporal autocorrelation in Y otherwise remained embedded in the Granger regression model. The GLS regression approach in this paper used just one measure of *gthi*, and whilst it accounting for the temporal auto-correlation, it did relate the response variable to defined lags in SMP and TEMP. More

onerous to compute than the fast omnibus Granger approach, piece-wise GLS regressions came closer to detecting and testing the real processes.

Wet and dry periods

In the wet period, the basic idea is that rainfall adequately replaced the water removed by trees in upward transport supporting evapotranspiration. Rainfall, indirectly through soil water supply (and some canopy wetting), met the demands of photosynthesis and growth. The system longer-term must achieve stability. When SMP_{-1} increased, i.e. became less negative, and *gthi* also increased, the coefficient was positive. Water became more readily available to the trees, and this can be interpreted as having led to a relaxation of any water stress limitation on girth increment. But when SMP_{-1} increased and *gthi* decreased, the coefficient was negative, and seemingly girth increment was being reduced even though the stress was being apparently relaxed. It cannot have been that increasing *gthi* lowered SMP_{-1} because SMP_{-1} preceded *gthi*, but water uptake was lowering SMP in the days(s) before, and this not at that earlier time showing an increase on *gthi*, constituted a 'delayed effect'. This explanation may go some way to solving the paradox.

Alternatively, for a small tree to have a negative *gthi*-SMP relationship indicated that increments at low SMP were larger than those at high SMP, i.e. the effect increasing SMP lowered *gthi*. This appears counter to the physics of water flow and stem expansion (Zweifel et al. 2001). It is highly unlikely that an understorey tree would lower SMP from high uptake (increased *gthi*) as would a large canopy one. Changing SMP with depth may be an explanation if the SMP these small trees experienced was the inverse of what was recorded at 20 cm depth, i.e. where SMP was high at the surface it was low at much lower depths and vice versa. The SMP at 20 cm depth acts as a reference level. This could be feasible if rain events were largely only wetting the top soil, or when dried out in the upper layers there was more water in the soil reachable by roots at depth. This would argue again for the critical

dependence of use of water on rooting depth. Further, it would mean that *gthi*-SMP correlations, positive and negative were reflecting 'normal' and inverse SMP scales. To accommodate this hypothesis, it is necessary also to consider large and small trees sharing the upper 20-40 cm of soil and SMP being well correlated across this depth range, then below, e.g. 40-100 cm small trees differentially separate out their roots to avoid competition, and lastly below 1-2 m the deeper roots of the larger trees (Jenik 1978).

When *gthi* increased with increased $TEMP_0$ though, the coefficient being positive, $TEMP_0$ may have caused the *gthi* change as a result of strong demand and uptake of water, later leading to swelling of the stem but only when, presumably, there was a sufficient supply coming from the soil (i.e. SMP_{-1} was near zero). Otherwise, when *gthi* decreased with increase in $TEMP_0$, the coefficient being negative, $TEMP_0$ could also have caused this too, but this was a situation where water was being rapidly taken up and supply was <u>not</u> being sufficiently met (SMP_{-1} was likely already low), and this would have caused the stems to shrink under the demand (Sheil 2003).

When water availability was non-limiting, that is SMP was quite high and near zero, transpiration would easily have proceeded, and when temperature was high, with little cloud cover and photosynthesis maximal, the girth would expand (Zimmermann 1983). In the dry period as SMP decreased transpiration and water became more limiting in the soil, but also the air in the canopy was drier, then stomatal closure would presumably have limited water loss, though nevertheless what water was being used would have caused a positive *gthi* when evapotranspiration increased. It might then be expected that the effect of evapotranspiration bypassed *gthi* (i.e. *gthi* did not alter) and directly affected SMP, so that lower rainfall and water uptake together affected SMP, and this latter then affected *gthi*. The control of water use in the crowns might explain why there was practically no significant interaction between SMP and TEMP on *gthi*. Predictions were that in the dry period the coefficient of *gthi* on

TEMP was lower than that in the wet period, because less water was fluxing. Then, in addition to that, the lower SMP would have decreased *gthi*, and the feedback between lower leaf potential and stomatal control would have gradually stepped down the demand over several days (Jones 1992). These lagged controls were subsumed within the time-series and very difficult to distinguish from effects of changing external factors.

In the dry period species' responses would be expected to have differed as those species running short of water attempted to still access it, and as supplies fell due to lower rainfall (*rft*), increased $TEMP_0$ would have resulted in lowered *gthi* (shrinkage). Lowered SMP_{-1} would have made the situation more acute. From wet to dry period the expectation was that coefficients for $TEMP_0$ became more negative, and coefficients for SMP_{-1} became for positive, compared with the wet period. This was not always the case, however. Other factors are important to consider here. (i) Some trees may have been accessing water at greater depths in the dry compared with wet period, and this would not have been reflected in top-soil SMP changes, these latter largely governed by recently declining rainfall. (ii) Trees which were large, with higher open crowns, might have been more influenced by the dry period than smaller trees with lower shaded crowns in the understorey.

Although there were slight differences on average in slopes of *gthi* on SMP_{-1} and $TEMP_0$ between ridge and lower-slope stations, these stations did not differ significantly in SMP, particularly in the dry period. In an earlier study in the same plots, (Gibbons and Newbery 2003) obtained very similar results and likewise reached the same conclusions. Differences in *gthi* responses between stations were much more likely to have been due to how root distribution changed vertically and horizontally with respect to the SMP profile. Differences in leaf water potentials in wet and dry periods were explained for the drought-tolerant *Dimorphocalyx muricatus*, growing mainly on ridges, by the fact that it had relatively little surface rooting and more roots with depth, whilst the drought-intolerant *Mallotus wrayi*,

growing across the whole topographic gradient, had conversely more roots near the surface and relatively few deeper ones (Gibbons and Newbery 2003). The SMP recorded at 20 cm depth in the present study was but an indicator of soil moisture status: SMP at lower depths were likely related to surface-layer SMP, albeit slightly differently for lower slopes and ridges depending on the maximum soil depths possible.

Possible role of competition

The small trees were forced to respond positively to increased TEMP like the larger ones, but they would additionally, presumably, have suffered from competition for water with them as their neighbours. The different species' time-series were in parallel, so the small tree increment changes are exactly concurrent with the those of the large trees. Hence what may appear matching in terms of the driving variables ($TEMP_0$ and SMP_{-1}) for the larger trees may not have been the case for the smaller understorey trees. Larger trees usually have both dense surface rooting, primarily for nutrient and water uptake, but also large deeper ones for access to additional water supplies in drier periods (e.g. (Stahl et al. 2013). Smaller understorey trees with their less deep roots were therefore highly likely, even inevitably, competing with the larger overstorey ones and this would have lowered the SMP they experienced locally.

Competition for below-ground resources is generally considered to be symmetric, i.e. trees take up water in proportion to their biomasses. However, differences between storeys lies not only in tree size but that the overstorey ones are much more lighted than understorey ones and this would lead competition for water to become more asymmetric. Nevertheless, correlations between coefficients and nearest neighbour basal area did not indicate evidence of a net competitive effects. This leads to two possible explanations: (i) Vertical root distributions differed significantly between large and small trees so that competition was ameliorated, and/or (ii) water was sufficiently redistributed laterally in the upper soil layers at night to obviate competitive effects. Deeper water could also have been available to the

shallower-rooted smaller trees by the process of hydraulic lift (see (Caldwell et al. 1991, Dawson 1993, Caldwell et al. 1998). Conversely, (Burgess et al. 1998, Burgess et al. 2001) suggested that water may be redistributed by roots downwards from rewetted surface soil to drier layers below. The relative strength of these equalizing processes would likely vary from time-to-time and place-to-place within the Danum plots depending on the precise neighbourhood of each tree. These processes would reinforce the competitive symmetry in water usage.

Above ground neighbour basal area may nevertheless not have been a good reflection of how root biomasses were distributed. Trees that then showed little difference between periods in their coefficients for SMP_{-1} and $TEMP_0$ would appear tolerant to the dry period: in the dry period they will have had higher evapotranspiration than in the wet one, this causing – at least in the short term – attempts to increase water uptake. This may not necessarily have lowered SMP_{-1} though. An understorey tree which was not close to a large canopy one might have had a positive SMP_{-1} coefficient, whilst when the trees were close to one another, in competition for water, it had a negative coefficient because <u>locally</u> it was suffering water limitation, although the overall, large-tree dominated, <u>average</u> SMP_{-1} was indicating otherwise. In other words, where small and large trees would have had similar *gthi* at low SMP_{-1}, when SMP_{-1} was closer to zero *gthi* for large trees was higher than at low SMP_{-1} (positive slope), whilst that for small trees *gthi* dropped lower (negative slope). SMP sensor values averaged across stations were effectively being re-weighted locally by the larger tree effects. These factors may account for the almost consistently positive coefficients in wet and dry periods for all trees' *gthi* with regard to TEMP but the mixed set of positive and negative coefficients (between and within species) in them with regard to SMP_{-1}.

If increasing *gthi* of small trees should always, as a principle, be positively related to the increasing SMP where its roots mostly access water, then the problematic might be 'stood

on its head', to show that those trees with decreasing relationships indicate rooting at deeper than the 20-cm reference. This might be a way of indirectly identifying rooting depths.

Complex water flux dynamics

In the dry period stomatal closure would doubtless have played a role in slowing evapotranspiration and restricting water uptake as SMP decreased (Jones 1992). However, the relatively slow dynamics involved are spread over many days, as first the tree water stores were utilized and then the potentials began to decrease throughout the tree from crown to roots. With insufficient new rainfall the low SMP would not have been relieved, and the interplay with *gthi* would, if conditions remained constant for a while, equilibrate at a new state, albeit a likely unstable one. Different trees at different locations in the forest would have reduced the soil moisture content to different degrees locally, and to different depths, resulting in a highly heterogeneous 3D distribution. This might have equilibrated spatially, particularly at night for the top 20 (-40) cm of the profile. For this reason, the responses of different individuals in the dry period would be expected to have been even more variable than in the wet one, the more stressful conditions in the dry, exacerbating the relatively more stable situation in the wet period. The corresponding wet and dry period responses were clearly not well correlated, even though the data were coming from the same individuals over time.

Using the same trees across the whole study will have inevitably confounded differences *gthi* and SMP between the wet and dry periods with changes in neighbourhood tree dynamics in one or other of the periods, e.g. if a tree died nearby or lost large branches, parts of the canopy changed due to large-tree deaths even further away. In a related way, the short periods of volatility in *gthi* shown by four of the banded trees were most likely due to either the measured tree itself losing a branch or otherwise suffering damage and readjusting its water flux balance, or just temporarily being affected by local neighbour tree dynamics.

If the hydraulic architecture of trees maps to a simple linear system, over time input 'on average' will balance output, with lags (Chatfield 2004). The swelling and shrinking of the stem is in a feedback loop with the increase and decrease in SMP in the soil. TEMP, as a proxy for photosynthesis and evapotranspiration pull, externally controls water uptake, and this water is replaced by inputs from rainfall. Rainfall therefore drove *gthi* change via SMP: "*rft* –> SMP <–> *gthi* <– TEMP". SMP and *gthi* were reciprocally coupled, and driven and stabilized by these two main external variables, *rft* and TEMP. If gthi is seen as an inverse measure of tree moisture potential (TMP), it entails an internal feedback loop between SMP and *gthi*. The two variables may be displaying a Lorenz manifold (Sugihara et al. 2012) in a way that mirage correlations are more or less strong on one or the other fold depending on whether *rft* or TEMP are having the relatively stronger external influence. The mix of positive and negative coefficients found within and between understorey species when fitting the *gthi* to SMP (but not for TEMP) in the GLS regressions — positive and negative correlations essentially, may have been a result of different individuals being 'caught' on different parts of a general attractor due to their particular set-up system circumstances in the time period studied. Some series showed a positive, others negative, correlation. This would appear a candidate set-up for convergent cross mapping. The shape of such a manifold might be different in wet and dry periods.

Confronting hypotheses

It was proposed by Newbery et al. (Newbery et al. 1999, Newbery et al. 2011) that the understorey trees might be divided into (a) the small juveniles of overstorey species, and (b) all trees of true understorey species, subdivided into (b1) drought-tolerant and (b2) drought-intolerant groups. The time-series analyses did not provide clear confirmation of traits related to water-flux related stem changes that would distinguish species in the proposed structural-dynamic guilds of understorey tree species at Danum (Newbery et al. 1999, Newbery et al.

2011). Individual trees within species behaved quite idiosyncratically. This is interpreted to mean that the relationship between *gthi* and changing SMP (driven by temperature on evapotranspiration and by rainfall input) depended on the exact constellation of each and every forest location and its conditions, particularly in this case the water fluxes of neighbouring trees. It could also mean that the proposed manifold dynamics were interacting with neighbour competitive effects.

There was moreover no case to be made for the predicted species in the drought-intolerant guild (*M. wrayi*) consistently showing water stress whilst those in the drought-tolerant one (*D. muricatus, L. beccarianum*) indicating different means of coping with the shortages, even though these species show markedly differing spatial distributions with respect to plot topography (Newbery et al. 1996). Possibly more indicative responses would have been recorded under much stronger drought conditions (Newbery and Lingenfelder 2004), ones that matched the stronger events in the past when selection may have operated also more strongly (Newbery et al. 2011). The varying responses by different individuals of the understorey species have been due to high plasticity in form and response within species, determined by local tree neighbourhood in terms of the complexities of tree rooting and soil moisture three dimensional distributions. Downward redistribution would favour the deeper-rooted *D. muricatus*, upward the shallower-rooted *M. wrayi.*

Determining species traits by reduction from the structure and dynamics of their structural guilds, and detecting these traits in the field from long time series of measurements of individuals did prove highly challenging and inconclusive. Investigations are stymied by the severe lack of detailed knowledge of the spatial extents of the constituent species' individual tree rooting systems and their physiologies. The technicalities involved are still quite primitive, and the need for replication of matching SMP recordings below ground is formidable. Knowledge of tropical forest root systems remains extremely limited. In recent

decades, little attempt was made to advance on the framework laid by (Jenik 1978). Just one, cutting-edge, study to estimate approximately rooting depths and lateral root distributions of trees in dipterocarp forest on road sides has been made by (Baillie and Mamit 1983).

The highly interrelated processes running in a time series of even such a relatively small model system with one feedback loop and two external drivers, had primary effects that were likely variably and asynchronously lagged, and there were secondary effects applying. This led to very complicated dynamics at the individual tree level. The changing neighbourhood variables added another important source of spatial and temporal variability (noise) at the population-community level, a form of stochasticity. The forest overall though was functioning in physical and physiological terms at the whole ecosystem level with relatively stable dynamics, subsuming and equilibrating all the minor instabilities and variations of the two lower (population/individual) levels. The physics of water redistribution by equilibration along gradients, diurnally and some several days with lags contributes to the amelioration of asymmetric competition for water below ground.

Funding. The dendroband field work was supported by the Swiss National Science Foundation (Grant 31003A-110250, 2006-2010) and the subsequent data analysis by the Chair for Vegetation Ecology, Bern. Comparative tree growth data used in this paper came from previous research also supported by the SNSF (Grant 3100-59088).

Acknowledgements. This work was part of the Royal Society of London's SE Asian Rain Forest Research Programme 1985-2015. We thank the Sabah Biodiversity Council and the Danum Valley Management Committee for permission to continue research at Danum. Dr R. C. Ong (Sabah Forest Department) kindly provided host support. We appreciate the assistance of Jamil Hanapi in monitoring the stations and handling data downloads and transfer on

several occasions, and of Saidih Samat and Anthony Karolus with the installation and maintenance of field equipment.

Author contributions. The research was conceived jointly by DMN and ML. ML undertook bulk of the field work and prepared the raw data files. DMN statistically analysed the data set, and very largely wrote the paper with inputs from ML. Both authors read, discussed and corrected the various versions.

Data Accessibility The time series data have been placed at the Dryad Digital Repository (DOI: 10.5061/dryad.ffbg79crj).

REFERENCES

Aiba, S. I., and K. Kitayama. 2002. Effects of the 1997-98 El Nino drought on rain forests of Mount Kinabalu, Borneo. Journal of Tropical Ecology **18**:215-230.

Baillie, I. C., and J. D. Mamit. 1983. Observations on rooting in mixed dipterocarp forest, central Sarawak. Malaysian Forester **46**:369-374.

Brockwell, P. J., and R. A. Davis. 2002. Introduction to time series and forecasting. 2nd edition. Springer, New York.

Burgess, S. S. O., M. A. Adams, N. C. Turner, and C. K. Ong. 1998. The redistribution of soil water by tree root systems. Oecologia **115**:306-311.

Burgess, S. S. O., M. A. Adams, N. C. Turner, D. A. White, and C. K. Ong. 2001. Tree roots: conduits for deep recharge of soil water. Oecologia **126**:158-165.

Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia **113**:151-161.

Caldwell, M. M., J. H. Richards, and W. Beyschlag. 1991. Hydraulic lift: ecological implications and water efflux from roots. Pages 423-436 *in* D. Atkinson, editor. Plant Root Growth: an ecological perspective. Blackwell Scientific Publishers, Oxford.

Cartwright, N. 2007. Hunting causes and using them. Cambridge University Press, Cambridge, UK.

Chatfield, C. 2004. The analysis of time series. Chapman and Hall/CRC, Boca Raton.

Chen, D., M. A. Cane, A. Kaplan, S. E. Zebiak, and D. J. Huang. 2004. Predictability of El Nino over the past 148 years. Nature **428**:733-736.

CPC. 2020. El Niño / Southern Oscillation (ENSO): Cold & Warm Episodes by Season. USA Government NOAA / National Weather Service, Climate Prediction Center, https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php.

Dawson, T. E. 1993. Hydraulic lift and water-use by plants: implications for water balance, performance and plant-plant interactions. Oecologia **95**:565-574.

Drew, D. M., and G. M. Downes. 2009. The use of precision dendrometers in research on daily stem size and wood property variation: A review. Dendrochronologia **27**:159-172.

Eichler, M. 2013. Causal inference with multiple time series: principles and problems. Philosophical Transactions of the Royal Society A - Mathematical Physical and Engineering Sciences **371**:1-17.

Enders, W. 2015. Applied economic time series. Fourth edition. Wiley, Hoboken, N. J., USA.

Fox, J. 2008. Applied regression analysis and generalized linear models. 2nd edition. Sage, Los Angeles.

Fox, J., and S. Weisberg. 2011. An R companion to Applied Regresson. 2nd edition. Sage, Los Angeles.

Garnier, E., and A. Berger. 1986. Effect of water stress on stem diameter changes of peach trees growing in the field. Journal of Applied Ecology **23**:193-209.

Gibbons, J. M., and D. M. Newbery. 2003. Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. Plant Ecology **164**:1-18.

Granger, C. W. J. 1969. Investigating causal relations by economic models and cross-spectral methods. Econometrica **37**:424-438.

Harrison, R. D. 2001. Drought and the consequences of El Nino in Borneo: a case study of figs. Population Ecology **43**:63-75.

Herzog, K. M., R. Hasler, and R. Thum. 1995. Diurnal changes in the radius of subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. Trees-Structure and Function **10**:94-101.

Hyndman, R. J., and Y. Khandakar. 2008. Automatic time series forecasting: The forecast package for R. Journal of Statistical Software **27**:1-22.

Irvine, J., and J. Grace. 1997. Continuous measurements of water tensions in the xylem of trees based on the elastic properties of wood. Planta **202**:455-461.

Itoh, A., S. Nanami, T. Harata, T. Ohkubo, S. Tan, L. Chong, S. J. Davies, and T. Yamakura. 2012. The effect of habitat association and edaphic conditions on tree mortality during El Nino-induced drought in a Bornean dipterocarp forest. Biotropica **44**:606-617.

Jenik, J. 1978. Roots and root systems in tropical trees: morphologic and ecologic aspects. Pages 323-349 *in* P. B. Tomlinson and M. H. Zimmermann, editors. Tropical trees as living systems. Cambridge University Press, Cambridge, U.K.

Jones, H. G. 1992. Plants and microclimate. Cambridge University Press, Cambridge, UK.

Kleinberg, S. 2013. Causality, probability and time. Cambridge University Press, Cambridge, UK.

Kozlowski, T. T., and C. H. Winget. 1964. Diurnal and seasonal variation in radii of some tree stems. Ecology **45**:149-&.

Lambers, H., F. S. Chapin, and T. L. Pons. 1998. Plant physiological ecology. Springer-Verlag, Berlin, Germany.

Lewis, S. L., P. M. Brando, O. L. Phillips, G. M. F. van der Heijden, and D. Nepstad. 2011. The 2010 Amazon Drought. Science **331**:554-554.

Lingenfelder, M., and D. M. Newbery. 2009. On the detection of dynamic responses in a drought-perturbed tropical rainforest in Borneo. Plant Ecology **201**:267-290.

Maindonald, J., and W. J. Braun. 2010. Data analysis and graphics using R. Cambridge University Press, Cambridge.

Mencuccini, M., T. Holtta, S. Sevanto, and E. Nikinmaa. 2013. Concurrent measurements of change in the bark and xylem diameters of trees reveal a phloem-generated turgor signal. New Phytologist **198**:1143-1154.

Monteith, J. L., and M. Unsworth. 1990. Principles of environmental physics. E. Arnold, London, UK.

Nakagawa, M., K. Tanaka, T. Nakashizuka, T. Ohkubo, T. Kato, T. Maeda, K. Sato, H. Miguchi, H. Nagamasu, K. Ogino, S. Teo, A. A. Hamid, and L. H. Seng. 2000. Impact of severe drought associated with the 1997-1998 El Nino in a tropical forest in Sarawak. Journal of Tropical Ecology **16**:355-367.

Newbery, D. M., E. J. F. Campbell, Y. F. Lee, C. E. Ridsdale, and M. J. Still. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **335**:341-356.

Newbery, D. M., E. J. F. Campbell, J. Proctor, and M. J. Still. 1996. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. Vegetatio **122**:193-220.

Newbery, D. M., D. N. Kennedy, G. H. Petol, L. Madani, and C. E. Ridsdale. 1999. Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. Philosophical Transactions of the Royal Society B-Biological Sciences **354**:1763-1782.

Newbery, D. M., and M. Lingenfelder. 2004. Resistance of a lowland rain forest to increasing drought intensity in Sabah, Borneo. Journal of Tropical Ecology **20**:613-624.

Newbery, D. M., and M. Lingenfelder. 2009. Plurality of tree species responses to drought perturbation in Bornean tropical rain forest. Plant Ecology **201**:147-167.

Newbery, D. M., and M. Lingenfelder. 2017. Progression and stability analysis of rain forest tree growth under environmental stochasticity. Ecosphere **8**:1-24.

Newbery, D. M., M. Lingenfelder, K. F. Poltz, R. C. Ong, and C. E. Ridsdale. 2011. Growth responses of understorey trees to drought perturbation in tropical rainforest in Borneo. Forest Ecology and Management **262**:2095-2107.

Newbery, D. M., and C. E. Ridsdale. 2016. Neighbourhood abundance and small-tree survival in a lowland Bornean rainforest. Ecological Research **31**:353-366.

Payne, R. W., S. A. Harding, D. A. Murray, and others. 2011. The Guide to GenStat Release 14, Part 1: Syntax and Data Management. Part 2: Statistics. VSN International, Hemel Hempstead, UK

Pelissier, R., and J. P. Pascal. 2000. Two-year tree growth patterns investigated from monthly girth records using dendrometer bands in a wet evergreen forest in India. Journal of Tropical Ecology **16**:429-446.

Peramaki, M., E. Nikinmaa, S. Sevanto, H. Ilvesniemi, E. Siivola, P. Hari, and T. Vesala. 2001. Tree stem diameter variations and transpiration in Scots pine: an analysis using a dynamic sap flow model. Tree Physiology **21**:889-897.

Pesonen, E., K. Mielikainen, and H. Makinen. 2004. A new girth band for measuring stem diameter changes. Forestry **77**:431-439.

Phillips, O. L., L. Aragao, S. L. Lewis, J. B. Fisher, J. Lloyd, G. Lopez-Gonzalez, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Banki, L. Blanc, D. Bonal, P. Brando, J. Chave, A. C. A. de Oliveira, N. D. Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jimenez, G. Lloyd, P. Meir, C. Mendoza, A.

Morel, D. A. Neill, D. Nepstad, S. Patino, M. C. Penuela, A. Prieto, F. Ramirez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. ter Steege, J. Stropp, R. Vasquez, P. Zelazowski, E. A. Davila, S. Andelman, A. Andrade, K. J. Chao, T. Erwin, A. Di Fiore, E. Honorio, H. Keeling, T. J. Killeen, W. F. Laurance, A. P. Cruz, N. C. A. Pitman, P. N. Vargas, H. Ramirez-Angulo, A. Rudas, R. Salamao, N. Silva, J. Terborgh, and A. Torres-Lezama. 2009. Drought Sensitivity of the Amazon Rainforest. Science **323**:1344-1347.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-plus. Springer, New York.

Pinheiro, J. C., D. M. Bates, D. Sarkar, and R_Development_Core_Team. 2013. nlme: linear and nonlinear mixed effects models. R package version 3.1-108. .

Potts, M. D. 2003. Drought in a Bornean everwet rain forest. Journal of Ecology **91**:467-474.

R_Core_Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Sevanto, S., T. Holtta, A. Hirsikko, T. Vesala, and E. Nikinmaa. 2005. Determination of thermal expansion of green wood and the accuracy of tree stem diameter variation measurements. Boreal Environment Research **10**:437-445.

Sevanto, S., E. Nikinmaa, A. Riikonen, M. Daley, J. C. Pettijohn, T. N. Mikkelsen, N. Phillips, and N. M. Holbrook. 2008. Linking xylem diameter variations with sap flow measurements. Plant and Soil **305**:77-90.

Sheil, D. 2003. Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by dendrometer bands. Canadian Journal of Forest Research **33**:2027-2035.

Simonneau, T., R. Habib, J. P. Goutouly, and J. G. Huguet. 1993. Diurnal changes in stem dimater depend upon variations in water content: direct eviden ce from peach trees. Journal of Experimental Botany **44**:615-621.

Stahl, C., B. Burban, F. Bompy, Z. B. Jolin, J. Sermage, and D. Bonal. 2010. Seasonal variation in atmospheric relative humidity contributes to explaining seasonal variation in trunk circumference of tropical rain-forest trees in French Guiana. Journal of Tropical Ecology **26**:393-405.

Stahl, C., B. Herault, V. Rossi, B. Burban, C. Brechet, and D. Bonal. 2013. Depth of soil water uptake by tropical rainforest trees during dry periods: does tree dimension matter? Oecologia **173**:1191-1201.

Steppe, K., D. J. W. De Pauw, and R. Lemeur. 2008. Validation of a dynamic stem diameter variation model and the resulting seasonal changes in calibrated parameter values. Ecological Modelling **218**:247-259.

Steppe, K., D. J. W. De Pauw, R. Lemeur, and P. A. Vanrolleghem. 2006. A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. Tree Physiology **26**:257-273.

Sugihara, G., R. May, H. Ye, C. H. Hsieh, E. Deyle, M. Fogarty, and S. Munch. 2012. Detecting Causality in Complex Ecosystems. Science **338**:496-500.

Tyree, M. T., and F. W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. New Phytologist **119**:345-360.

Van Nieuwstadt, M. G. L., and D. Sheil. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. Journal of Ecology **93**:191-201.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. 4th edition. Springer, Berlin.

Vincent, G., H. de Foresta, and R. Mulia. 2009. Co-occurring tree species show contrasting sensitivity to ENSO-related droughts in planted dipterocarp forests. Forest Ecology and Management **258**:1316-1322.

Walsh, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. Journal of Tropical Ecology **12**:385-407.

Walsh, R. P. D., and D. M. Newbery. 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. Philosophical Transactions of the Royal Society B-Biological Sciences **354**:1869-1883.

Wang, J., and T. W. Sammis. 2008. New automatic band and point dendrometers for measuring stem diameter growth. Applied Engineering in Agriculture **24**:731-742.

Whickam, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York.

Zeileis, A., and G. Grothendieck. 2005. zoo: S3 infrastructure for regular and irregular time series. Journal of Statistical Software **14**.

Zimmermann, M. H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Germany.

Zweifel, R. 2016. Radial stem variations - a source of tree physiological information not fully exploited yet. Plant Cell and Environment **39**:231-232.

Zweifel, R., H. Item, and R. Hasler. 2001. Link between diurnal stem radius changes and tree water relations. Tree Physiology **21**:869-877.

Zweifel, R., L. Zimmermann, and D. M. Newbery. 2005. Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiology **25**:147-156.

Zweifel, R., L. Zimmermann, F. Zeugin, and D. M. Newbery. 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. Journal of Experimental Botany **57**:1445-1459.

Legends to Figures

Fig. 1. Positions of the eDDs trees in main plot 2 at Danum at the four stations. The small plus signs indicate the positions of the loggers. Closed colored symbols, scaled to tree stem girth (gbh, in cm), show the species of tree used (Table 1): codes for them are listed in Table 2. The open crossed symbols indicate the two tree (g13, g21) that were omitted from the analyses.

Fig. 2. Running 30-day rainfall totals at Danum over the dendroband study period, showing the wet and dry periods used, between the green and red vertical dashed lines respectively.

Fig. 3. Mean diurnal change in tree girth (*gthch*), integrated for 48 half-hour time intervals referenced daily to 00:00, expressed per mille, for each of 20 originally selected trees. Two trees' series (see Fig. 1) were insufficient and were later omitted. Panel headers: following the band codes, are species codes and, in parenthesis, tree size classes (*scl*), as listed in Table 2. The solid black curves are the means of the 30 18-day sub-periods of the wet period and the black dashed lines their 95% confidence limits. The dotted colored curves are the three sub-periods of the dry period. Positive values of *gthch* indicate stem swelling, and negative ones, stem shrinkage. Each successive row of panels is for stations 1 to 4, each row with its four-five trees (see Table 2).

Fig. 4. Mean ± SE coefficients (slopes) of *gthi* regressed on soil moisture potential, SMP, at 0-, 1- and 2-day lags, in the wet (green bar) and dry (orange bar) periods for the 18 trees taken for the time-series analyses. There were no dry-period estimates for station 4 (see text for explanation). Bands are listed in Table 4 with individual tree codes.

Fig. 5. Mean ± SE coefficients (slopes) of *gthi* regressed on logger temperature, TEMP, at 0-, 1- and 2-day lags, in the wet (green bar) and dry (orange bar) periods for the 18 trees taken for the time-series analyses. There were no dry-period estimates for station 4 (see text for explanation). Bands are listed in Table 4 with individual tree codes.

Fig. 6. Mean and standard deviation (sd) of daily girth increments (*gthi*), plotted against stem girth (*gbh*) in the wet (a, c; n = 18) and dry (b, d; n = 13) periods. Species symbols are color-coded, their abbreviations as labels with the individuals distinguished by numbers, are listed in Table 2. Size classes: *scl* 1, circles; 2, triangles.

Fig. 7. Standardized SMP_{-1} versus $TEMP_0$ coefficients graphed together for (a) wet and (b) dry periods for the 18 respective 13 trees analyzed for their gth_i time-series, and their corresponding dry- and wet-period (c) SMP_{-1} and (d) $TEMP_0$ values against one another. Symbols as in Fig. 6.

Fig. 8. Standardized SMP_{-1} and $TEMP_0$ coefficients plotted in relation to canopy status (*CanStat*), in (a, c) wet (n = 18), and (b, d) dry (n = 13), periods. Symbols as in Fig.6.

Fig. 9. Standardized SMP_{-1} and $TEMP_0$ coefficients in the wet period in relation to the corresponding (a, c) minimum and (b, d) maximum diurnal girth changes (*gthch*) of the periods (n = 18). Symbols as in Fig.6.

Fig. 10. Standardized SMP_{-1} and $TEMP_0$ coefficients in the dry period in relation to the corresponding (a, c) minimum and (b, d) maximum diurnal girth changes (*gthch*) of the periods (n = 13). Symbols as in Fig.6.

List of supplementary material

Appendix 1. Rainfall, soil moisture potential and temperature relationships; fitted coefficients, and cross-comparisons, influence of station, and Granger test results.

Appendix 2. Time-series graphs of mean soil moisture potential, ambient temperature, and tree girth increments in wet and dry periods.

Appendix 3. Tabulated *t*-values and their significances for all GLS-arima model fits, one and two-term, for wet and dry periods.

Appendix 4. Estimated SMP and TEMP coefficients from two-term GLS-arima regressions, for lags = 0 or 1 day.

Table 1. Species and numbers of trees selected for the electronic dendroband study at Danum (eDDS), and their distribution with topography.

			number		
Species	Family[1]	Storey[2]	lower slope	ridge	all
Dimorphocalyx muricatus (Hook. f.) Airy Shaw	Euph	U	1	3	4
Lophopetalum beccarianum Pierre	Cela	U	1	1	2
Mallotus wrayi King ex Hook. f.	Euph	U	3	1	4
Parashorea malaanonan Merr.	Dipt	O	1	2	3
Shorea fallax Meijer	Dipt	O	3	1	4
Shorea parvifolia Dyer	Dipt	O	1	2	3
Totals			10	10	20

[1] Dipt: Dipterocarpaceae; Euph: Euphorbiaceae; Cela: Celastraceae

[2]: O: overstorey species; U: understorey species (OUI)

Table 2. Details of the 18 selected trees and their electronic bands (eDDS), with species names and codes, reference tags, sizes (*gbh*, cm) at start of recording (March 2007) and corresponding size classes (*dcl*), three measures of canopy exposure (layer, space and light level – defined in the footnotes), these last averaged into a canopy status (canStat) value, and relative growth rates (*rgr*) for the wet and dry periods. Two of the original 20 trees could not be used (g13 and g21: see main text).

Station	tree	tag	Species name	Code	Band	Gbh (cm)	scl	Canopy layer[1]	space[2]	light[3]	CanStat	Rgr in P_3 (mm/m/yr)
1	1	560	*M. wrayi*	Mw	g11	31	1	2	2	2	2.00	14.01
1	2	567	*S. fallax*	Sf	g12	97	2	4	4.5	5	4.50	49.70
1	4	577	*L. beccarianum*	Lb	g14	31	1	2.5	3	3	2.83	20.62
1	5	1084	*S. fallax*	Sf	g15	27	1	2	3	1.5	2.17	10.84
2	2	1662	*P. malaanonan*	Pm	g22	74	2	3.5	3.5	3.5	3.50	8.96
2	3	1732	*D. muricatus*	Dm	g23	30	1	2	3	2	2.33	9.36
2	4	1685	*M. wrayi*	Mw	g24	34	1	2	3	3	2.67	10.69
2	5	2405	*S. fallax*	Sf	g25	33	1	2	2	2.5	2.17	23.85
3	1	7680	*M. wrayi*	Mw	g31	34	1	2.5	2	2	2.17	9.33
3	2	6892	*S. parvifolia*	Sp	g32	78	2	4	4	4.5	4.17	55.42
3	3	6900	*L. beccarianum*	Lb	g33	39	1	3	2.5	2.5	2.67	33.91
3	4	7436	*D. muricatus*	Dm	g34	39	1	2	2.5	3	2.50	2.11

3	5	7586	*D. muricatus*	Dm	g35	48	1	2	3	1.5	2.17	0.00
4	1	8077	*S. fallax*	Sf	g41	31	1	2	2.5	2	2.17	0.00
4	2	8060	*D. muricatus*	Dm	g42	33	1	2.5	2	1.5	2.00	0.00
4	3	8321	*P. malaanonan*	Pm	g43	117	2	4	4	4	4.00	12.30
4	4	8848	*S. parvifolia*	Sp	g44	97	2	4	4	4.5	4.17	18.94
4	5	8810	*P. malaanonan*	Pm	g45	69	2	3	4	3.5	3.50	8.92

[1] Layer of tree: 1 tree-let; 2 understorey; 3 mid-level; 4 top canopy; 5 emergent.

[2] Space of crown: 1, completely suppressed; 2, mixed/entangled from all sides; 3, significantly overlapping most sides; 4, stems touching from some sides or above; 5, crown free, unshaded; by neighbours.

[3] Light level: 1 < 30%; 2, 30 - < 50%; 3, 50 - < 70%; 4, 70 - < 90; 5, ≥ 90% of crown receiving full light

Table 3. Correlations (Pearson's *r*) between the microclimatic variables recorded at the stations (mean soil water potential, SMP_0 [sqrt-transformed]; and logger temperature at 14:00 h, temp14L) and climatic variables recorded at the Danum Valley Field Centre – or derived from them (10-, 20-, 30- and 40-d running rainfall totals, rain10rft to rain50rft, from daily rainfall [sqrt-transformed]; dry-bulb temperature at 14:00, temp14; and maximum daily temperature, temp-max), for the wet and dry eDDs series. All correlations are significant at $P \leq 0.001$.

		wet			dry		
variables:		*r*	*t*	*n*	*r*	*t*	*n*
smpm	rain10rft	0.681	21.74	550	0.776	12.05	98
	rain20rft	0.553	15.53		0.782	12.30	
	rain30rft	0.501	13.56		0.761	11.49	
	rain40rft	0.485	12.97		0.756	11.33	
	rain50rft	0.557	15.70		0.741	10.81	
smpm	temp14L	−0.389	−9.89	550	−0.449	−4.92	98
	temp14	−0.225	−4.36	357	−0.311	−2.64	67
	temp-max	−0.254	−5.97	520	−0.361	−3.77	97
temp14L	temp14	0.739	20.64	357	0.713	8.21	67
	temp-max	0.747	25.58	520	0.818	13.85	97
temp14	temp-max	0.664	16.30	340	0.716	8.200	66

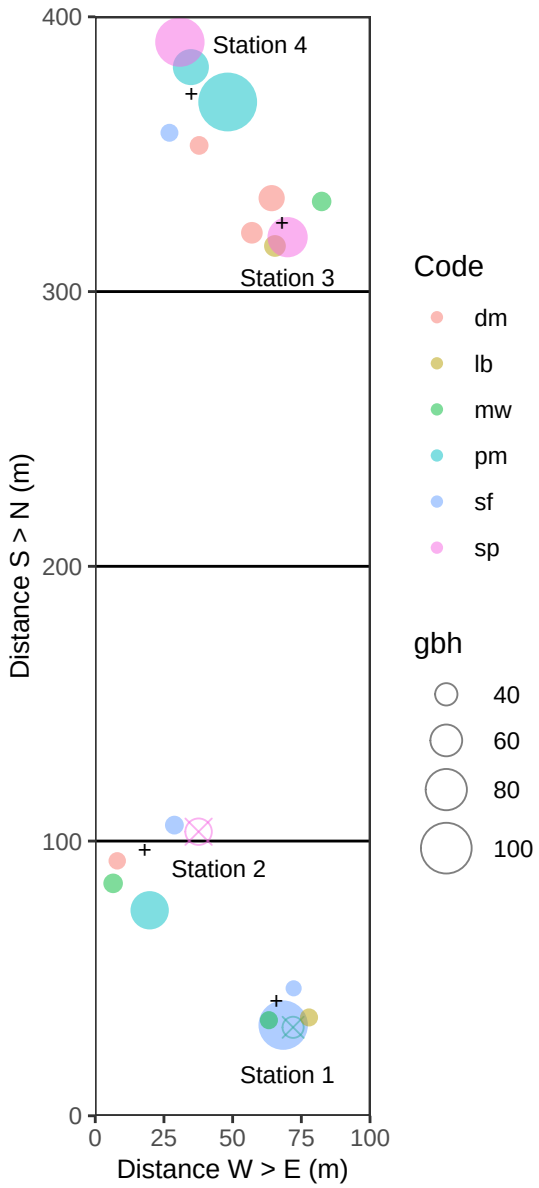
Table 4. Means, with standard deviations and lower and upper quartiles, of the 1-day girth increment, *gthi*, for the wet (n = 550) and dry (n = 93-98; see text) periods. Values are *gthi* in cm x 1000. Codex, are the codes in Table 2, with individuals within species numbered.

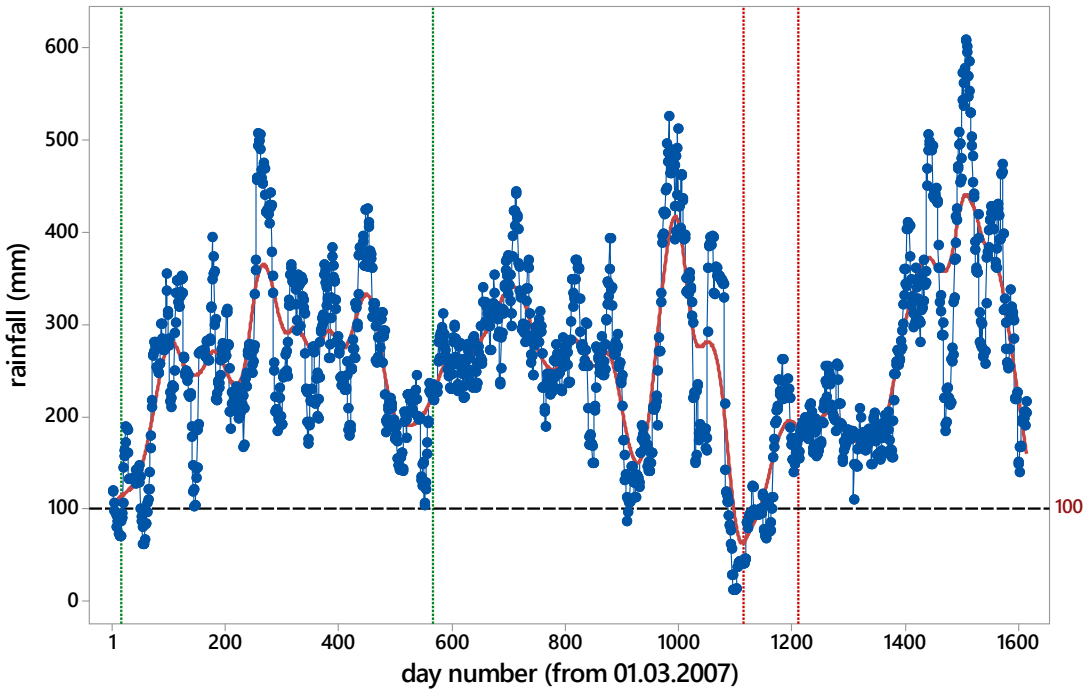
nr	station	tree	Codex	band	wet				dry			
					mean	sd	q1	q3	mean	sd	q1	q3
1	1	1	Mw1	g11	0.589	9.681	−4.0	6.5	1.623	8.564	−2.9	5.5
2	1	2	Sf1	g12	8.320	30.850	−9.6	23.2	1.128	4.692	−2.1	4.6
3	1	4	Lb1	g14	0.540	23.500	−4.9	6.0	0.770	13.110	−6.4	2.8
4	1	5	Sf2	g15	−0.451	14.875	−9.4	9.5	−1.480	14.950	−12.0	8.3
5	2	2	Pm1	g22	0.840	23.860	−5.0	5.4	−0.628	8.915	−6.3	3.1
6	2	3	Dm1	g23	0.097	9.347	−4.0	4.6	0.210	6.591	−4.6	5.0
7	2	4	Mw2	g24	−0.170	4.264	−2.7	1.9	1.369	8.674	−3.3	4.4
8	2	5	Sf3	g25	−0.240	10.505	−6.0	6.5	−0.560	11.560	−7.1	5.2
9	3	1	Mw3	g31	−0.057	4.655	−2.7	2.3	2.450	18.180	−5.6	6.9
10	3	2	Sp1	g32	7.397	10.933	0.6	14.6	5.996	5.298	3.0	10.2
11	3	3	Lb2	g33	2.470	4.047	−0.2	4.6	3.571	7.780	−1.3	7.4
12	3	4	Dm2	g34	−0.240	4.919	−3.3	2.7	0.929	5.310	−3.0	5.2

13	3	5	Dm3	g35	0.035	13.139	−5.6	6.6	0.277	7.099	−4.0	5.6
14	4	1	Sf4	g41	−0.090	3.493	−1.9	1.7	–	–	–	–
15	4	2	Dm4	g42	0.001	4.024	−2.3	2.3	–	–	–	–
16	4	3	Pm2	g43	3.831	22.445	−8.1	13.1	–	–	–	–
17	4	4	Sp2	g44	3.641	9.459	−1.9	8.7	–	–	–	–
18	4	5	Pm3	g45	−0.933	10.674	−6.3	3.7	–	–	–	–

Table 5. Mean adjusted coefficients for *Dimorphocalyx muricatus* (Dm) and *Mallotus wrayi* (Mw) from the time series GLS regressions of 1-day girth increment (*gthi*) on soil moisture potential lagged by 1 day (SMP_{-1}) and unlagged ambient temperature ($TEMP_0$), in the wet and dry periods. Individual replicate tree values are plotted in Fig. 7 which displays the species' ranges.

		wet		dry	
variable	species	n	coeff.	n	coeff.
SMP_{-1}	Dm	4	0.767	3	−0.043
	Mw	3	0.619	3	−0.397
$TEMP_0$	Dm	4	1.771	3	−0.133
	Mw	3	1.076	3	0.970


400
300
200
100
0
Station 4
Station 3
Station 2
Station 1
0
25
50
75
100
Distance W > E (m)
Distance S > N (m)
Code
dm
lb
mw
pm
sf
sp
gbh
40
60
80
100


rainfall (mm)
600
500
400
300
200
100
0
100
1
200
400
600
800
1000
1200
1400
1600
day number (from 01.03.2007)

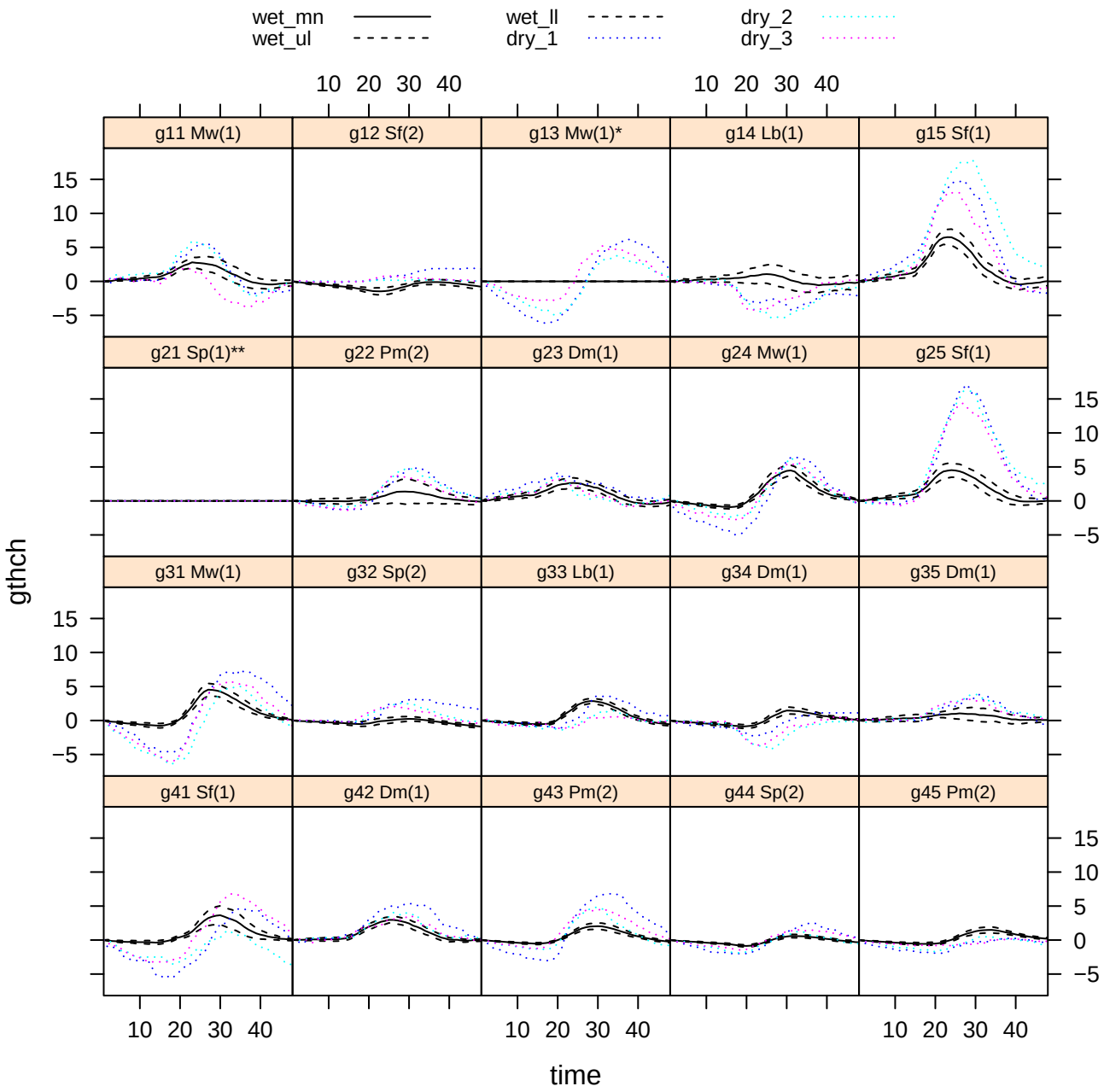

wet_mn
wet_ul
wet_ll
dry_1
dry_2
dry_3
g11 Mw(1)
g12 Sf(2)
g13 Mw(1)*
g14 Lb(1)
g15 Sf(1)
g21 Sp(1)**
g22 Pm(2)
g23 Dm(1)
g24 Mw(1)
g25 Sf(1)
g31 Mw(1)
g32 Sp(2)
g33 Lb(1)
g34 Dm(1)
g35 Dm(1)
g41 Sf(1)
g42 Dm(1)
g43 Pm(2)
g44 Sp(2)
g45 Pm(2)
gthch
time

Fig_4 − page 1

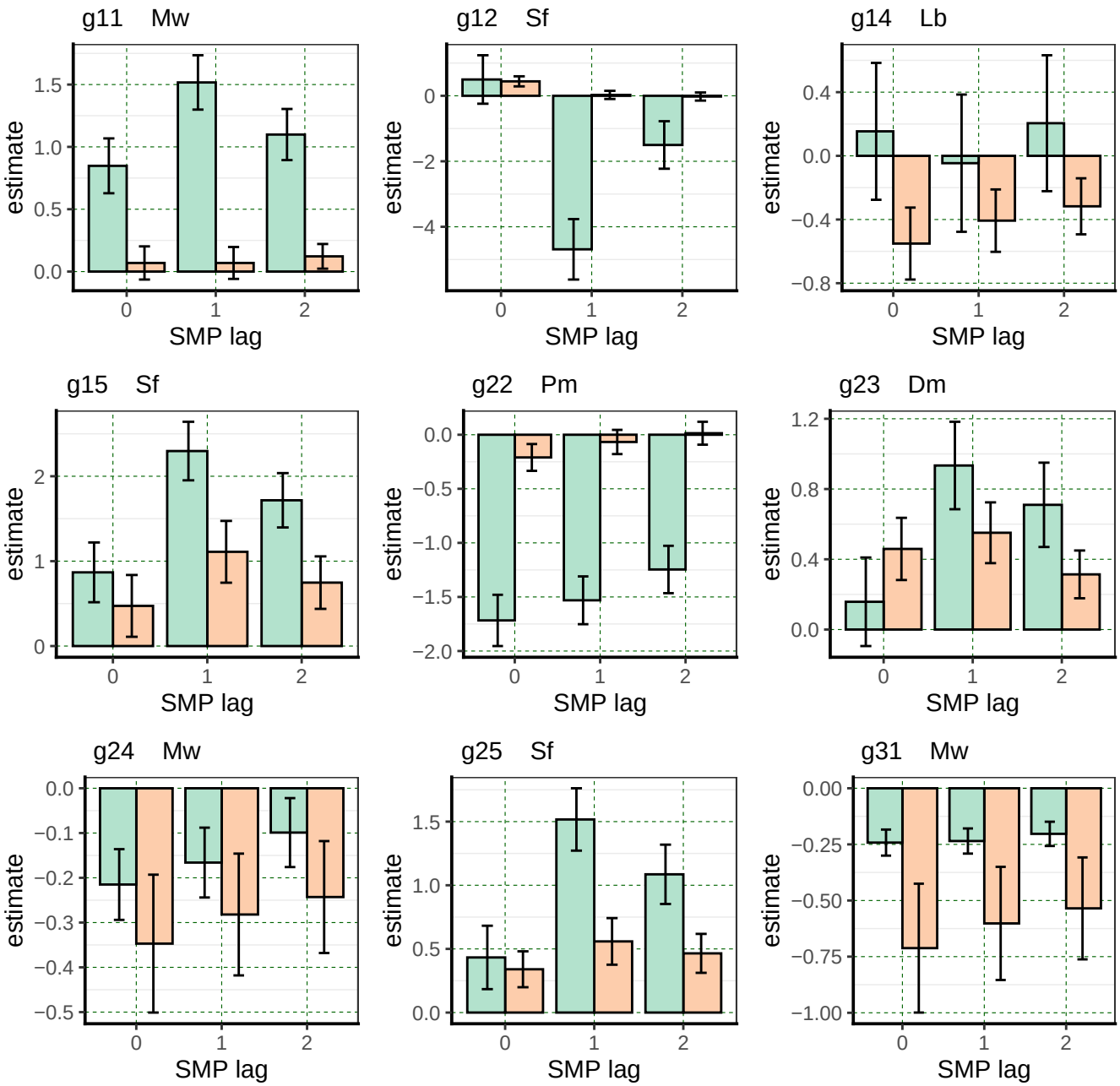

g11 Mw
g12 Sf
g14 Lb
g15 Sf
g22 Pm
g23 Dm
g24 Mw
g25 Sf
g31 Mw
estimate
SMP lag

Fig_4 − page 2

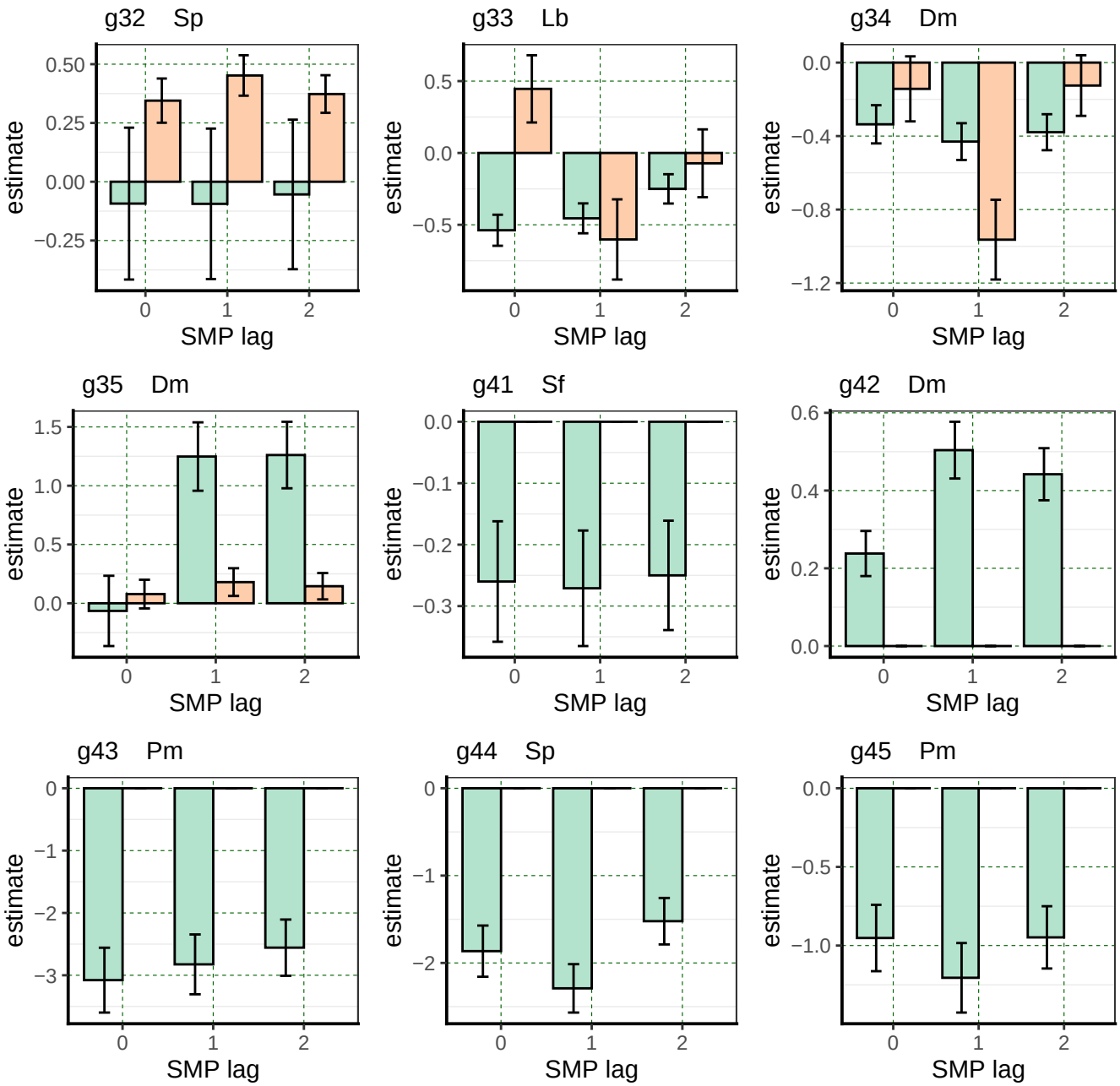

g32 Sp
g33 Lb
g34 Dm
g35 Dm
g41 Sf
g42 Dm
g43 Pm
g44 Sp
g45 Pm
estimate
SMP lag

Fig_5 − page 1

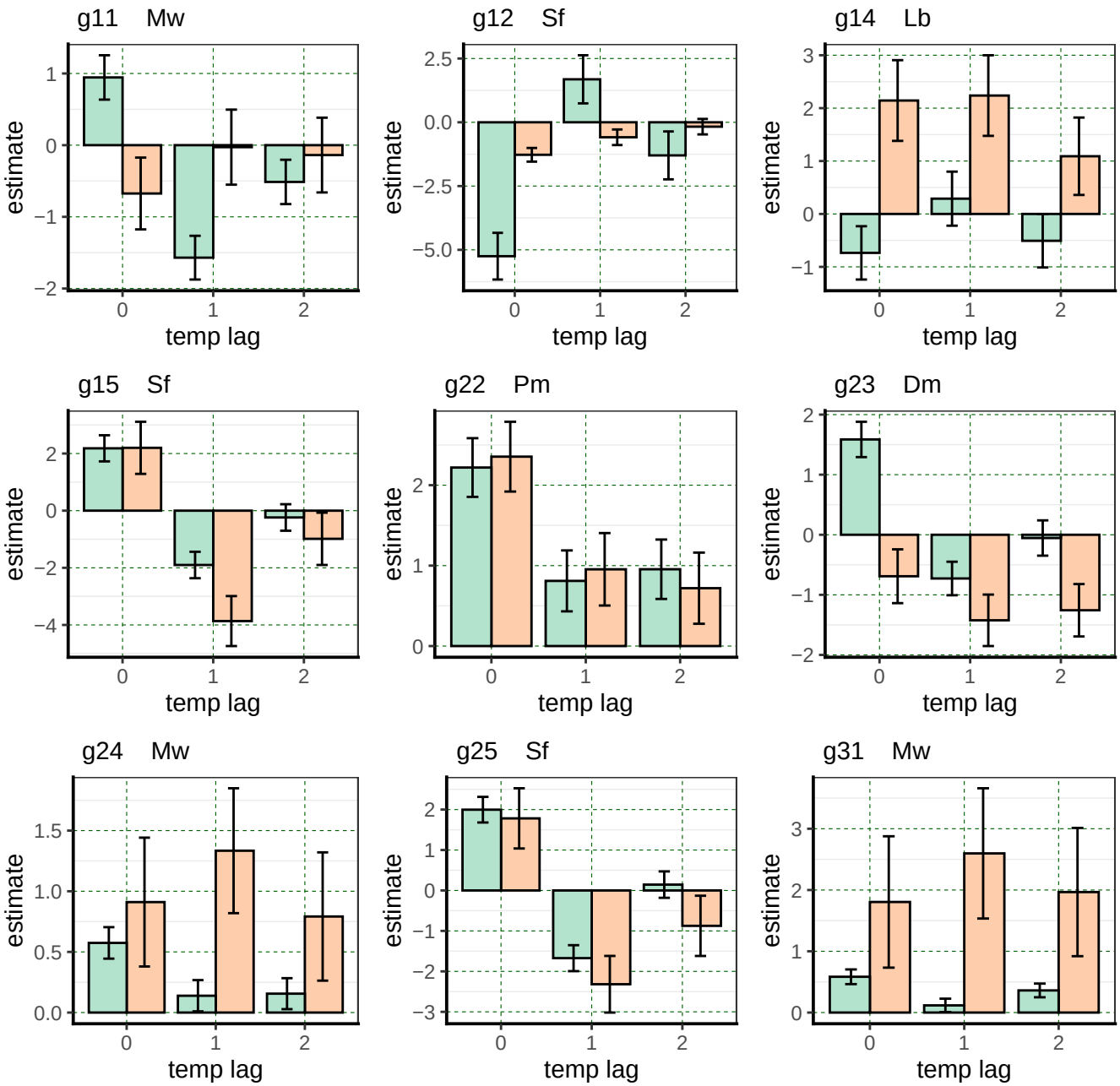

g11 Mw
g12 Sf
g14 Lb
g15 Sf
g22 Pm
g23 Dm
g24 Mw
g25 Sf
g31 Mw
estimate
temp lag

Fig_5 − page 2

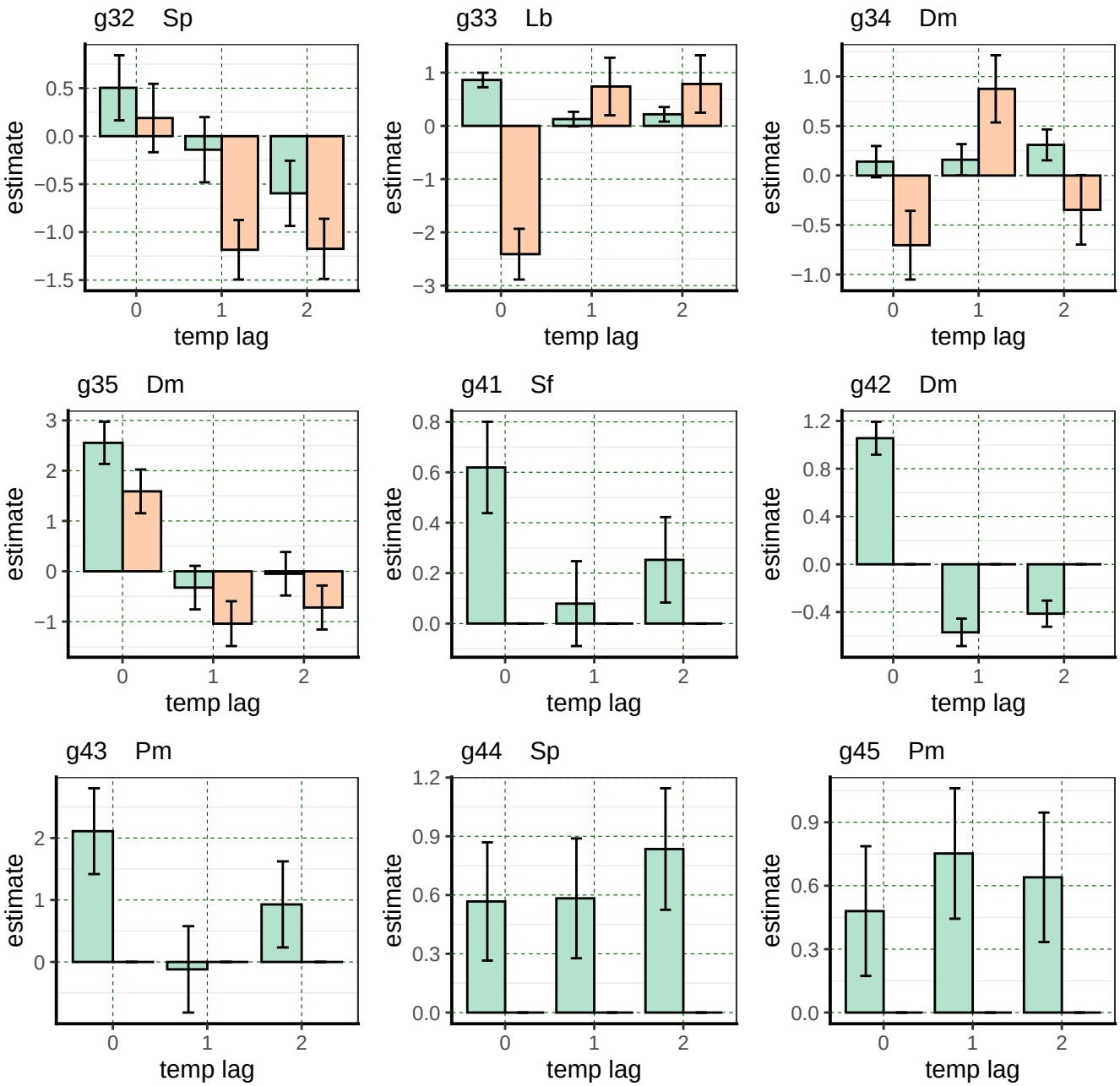

g32 Sp
g33 Lb
g34 Dm
g35 Dm
g41 Sf
g42 Dm
g43 Pm
g44 Sp
g45 Pm
estimate
temp lag

Fig. 6(a) Wet mean

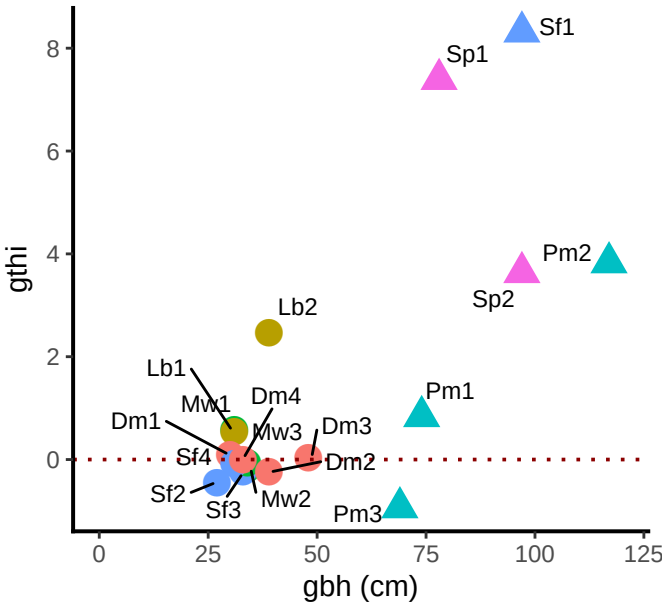


Fig. 6(c) Dry mean

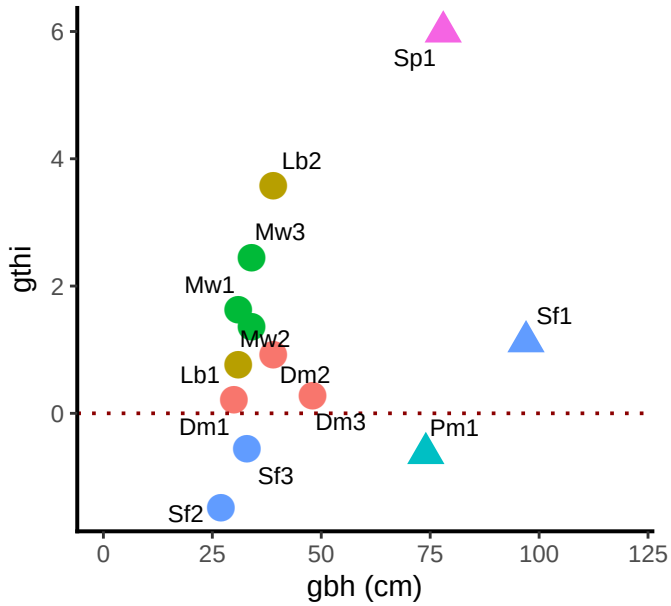


Fig. 6(b) Wet sd

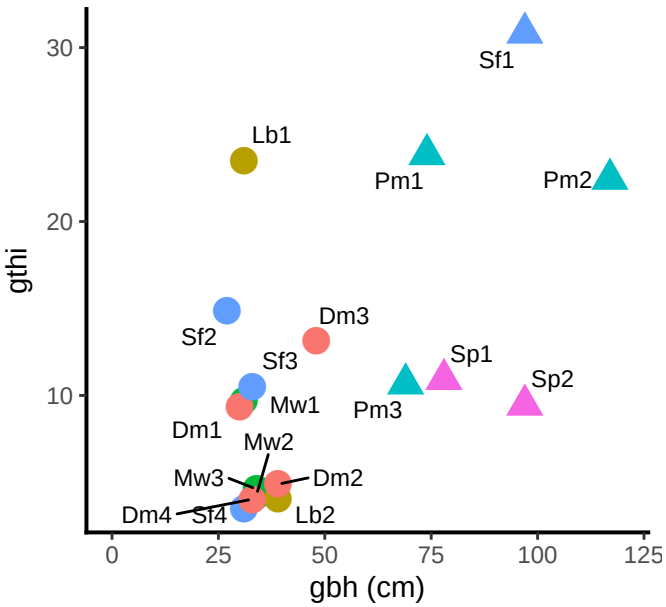


Fig. 6(d) Dry sd

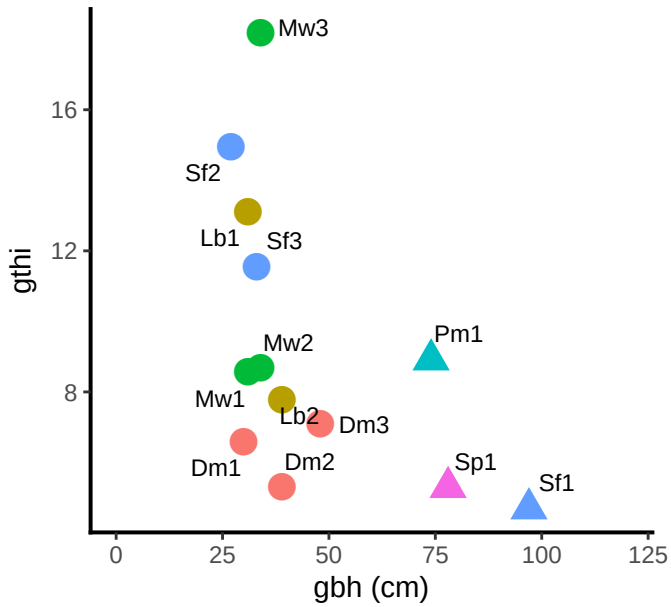


Fig. 7(a) Wet

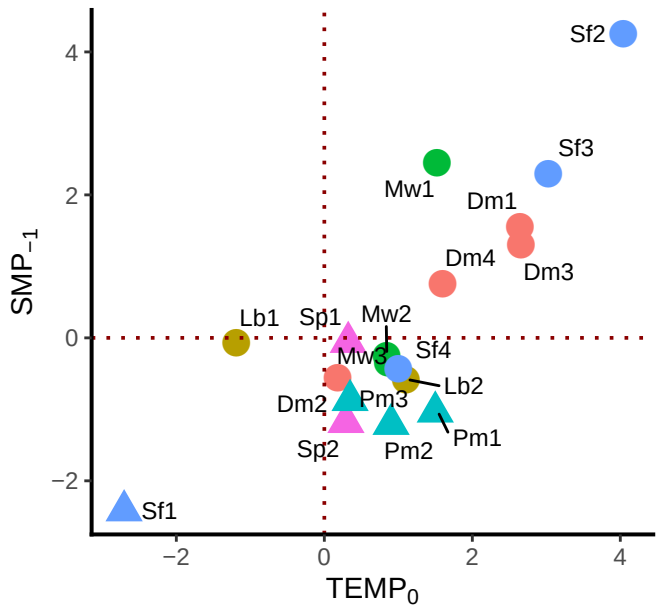


Fig. 7(b) Dry

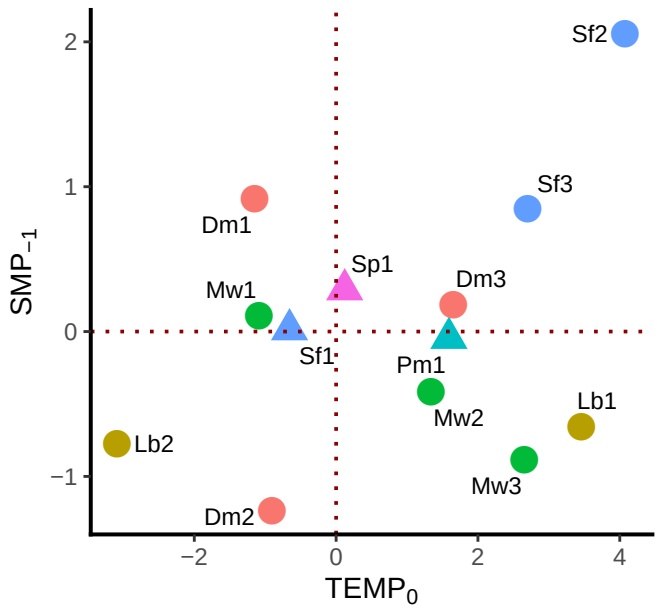


Fig. 7(c) SMP

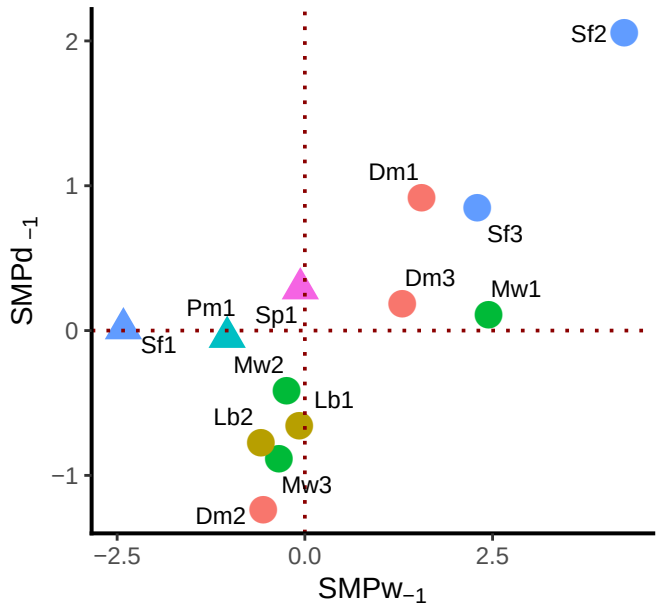


Fig. 7(d) TEMP

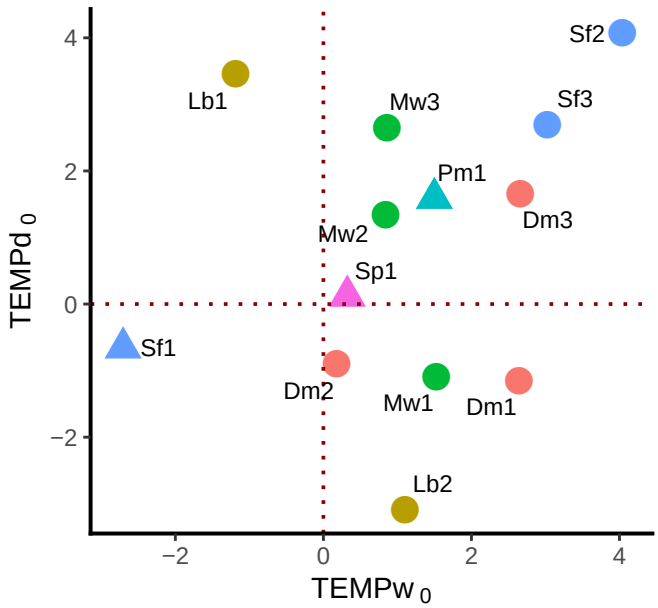


Fig. 8(a) Wet SMP and CanStat

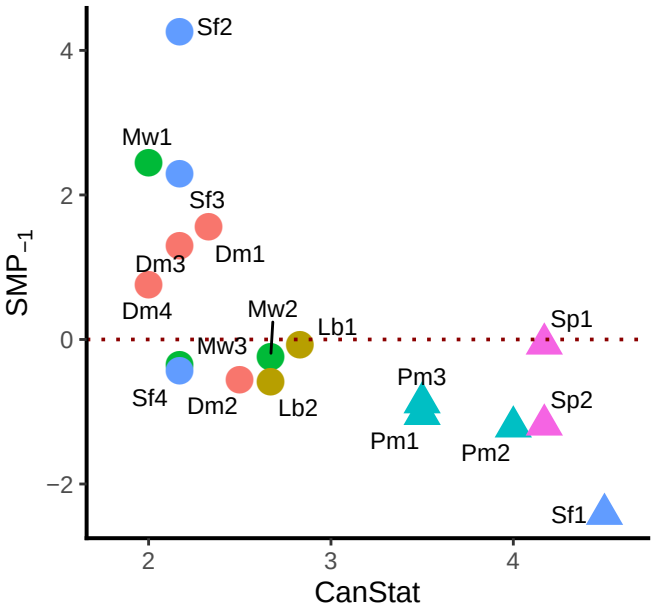


Fig. 8(b) Dry SMP and CanStat

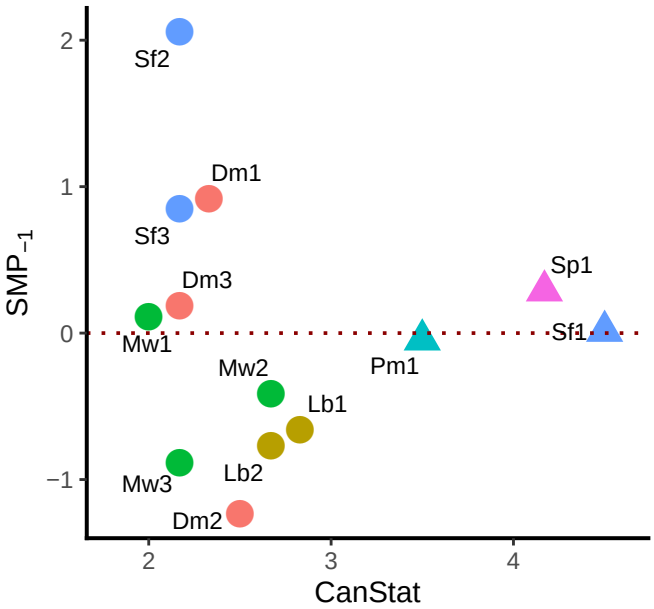


Fig. 8(c) Wet TEMP and CanStat

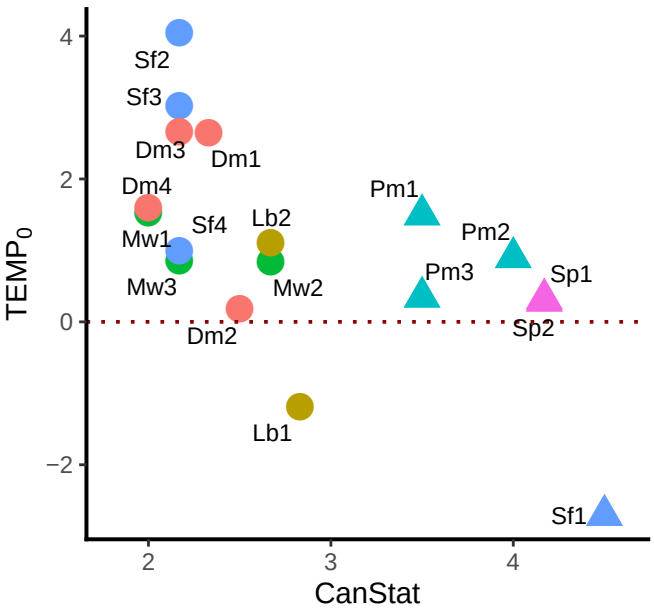


Fig. 8(d) Dry TEMP and CanStat

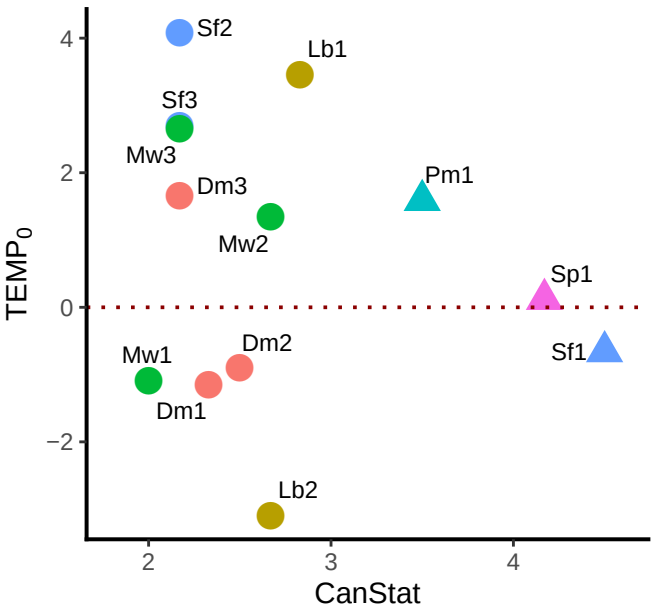


Fig. 9(a) Wet SMP and diurnal min

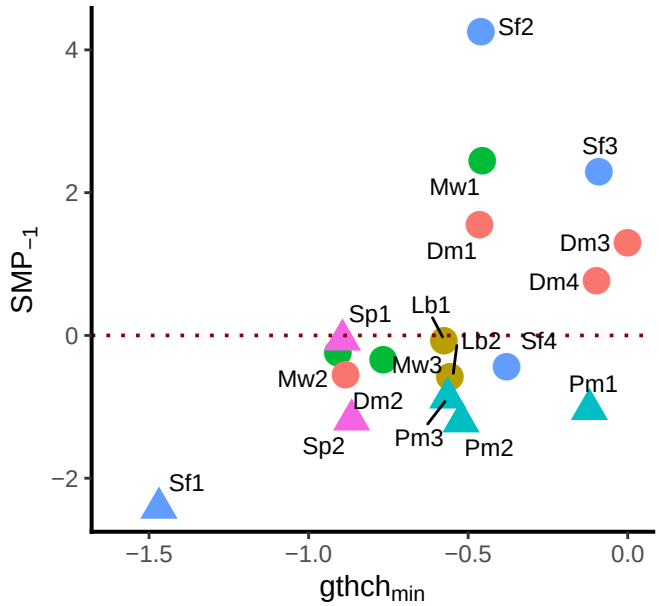


Fig. 9(b) Wet SMP and diurnal max

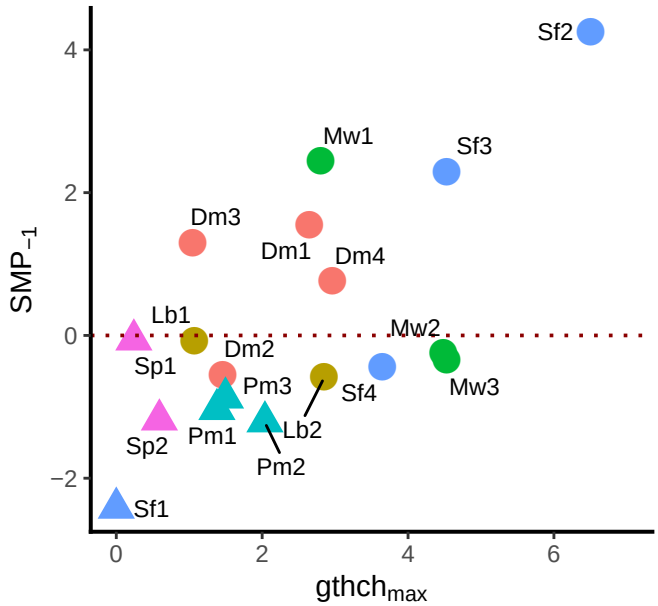


Fig. 9(c) Wet TEMP and diurnal min

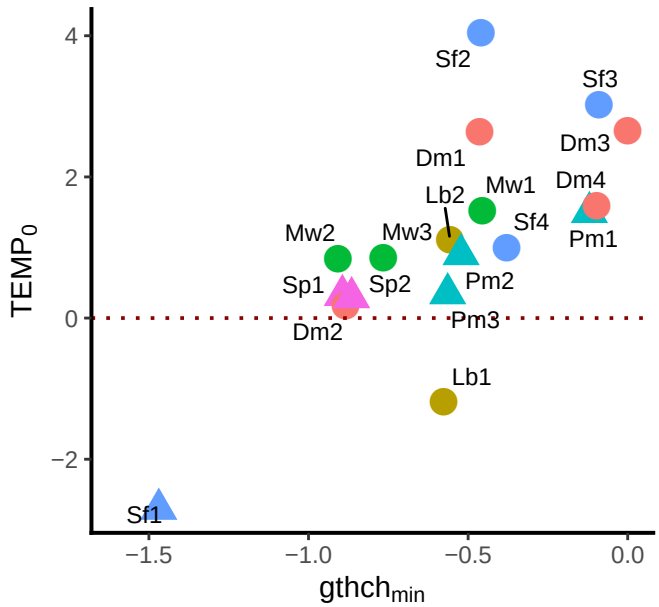


Fig. 9(d) Wet TEMP and diurnal max

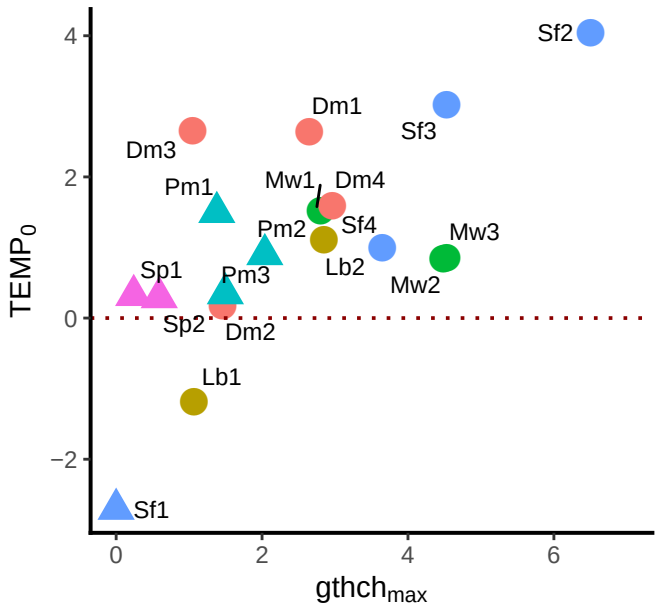


Fig. 10(a) Dry SMP and diurnal min

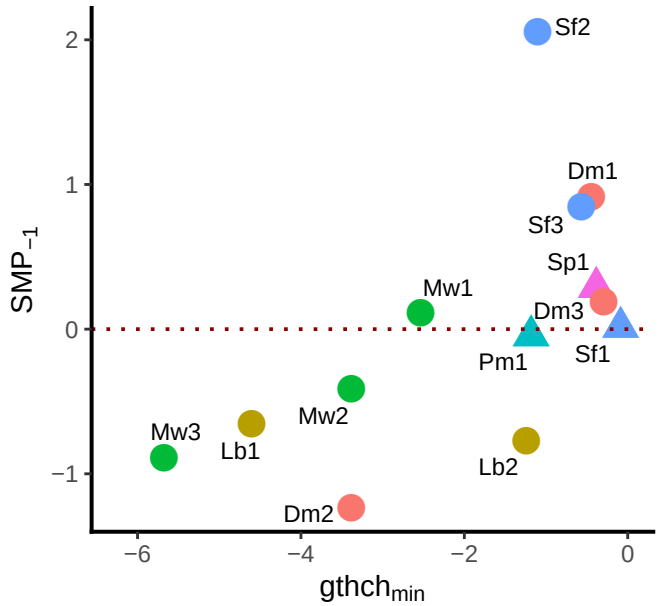


Fig. 10(b) Dry SMP and diurnal max

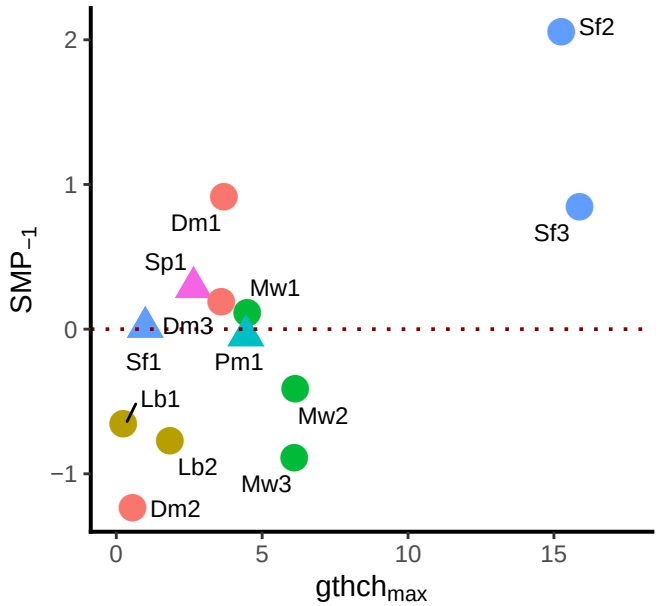


Fig. 10(c) Dry TEMP and diurnal min

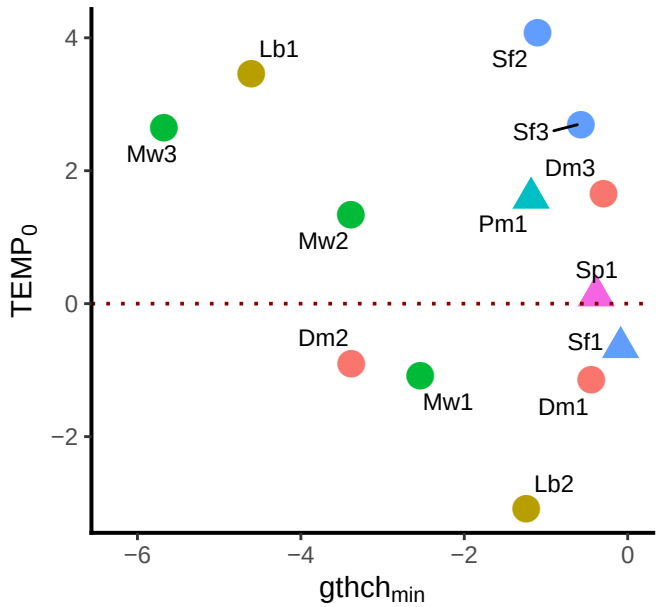
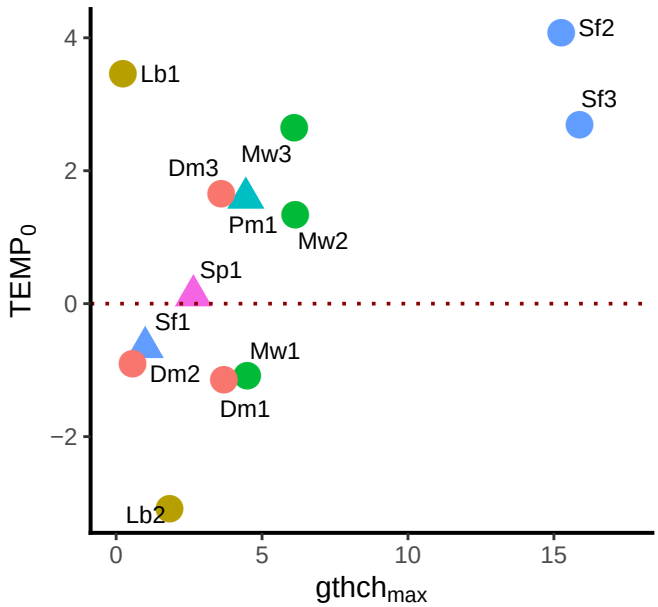



Fig. 10(d) Dry TEMP and diurnal max