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The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula

J. L. Baltzer*[,1], **S. J. Davies**[1,2], **S. Bunyavejchewin**[3] **and N. S. M. Noor**[4]

[1]*Center for Tropical Forest Science – Arnold Arboretum Asia Program, Harvard University Herbaria, Harvard University, Cambridge, MA 02138, USA;* [2]*Center for Tropical Forest Science, Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Panama, Panama;* [3]*Thai National Parks Wildlife and Plant Conservation Department, Research Office, Chatuchak, Bangkok 10900, Thailand; and* [4]*Forest Research Institute Malaysia, Kepong 52109, Selangor, Malaysia*

Summary

1. Patterns of water availability are frequently implicated in local and regional tree species distributions. A major floristic and climatic transition from aseasonal to seasonal evergreen tropical forest is the Kangar–Pattani Line (KPL) in the Indo-Sundaic region of Southeast Asia. We hypothesize that differences in species' drought tolerance will correspond with their distribution with respect to the KPL. Using a common garden study, we assess the role of differences in physiological drought tolerance traits to geographic distributions for 24 tropical tree species in relation to rainfall seasonality.

2. Inherent differences in desiccation tolerance of seedlings were quantified as water potentials and relative water contents (RWCs) below which the plant could no longer support living tissue, and plant water relation parameters were measured using pressure–volume analysis. The relationships among these traits were examined using bivariate trait relationships and a principal components analysis (PCA). The physiological traits contributing most to lethal water potential and RWC were assessed using multiple regression analysis.

3. Distribution-related differences in all desiccation tolerance and pressure–volume traits were detected both with and without phylogenetic correction. Widespread species that occurred in seasonally dry forests were able to maintain living tissue at more negative water potentials and lower RWCs than were species restricted to aseasonal forests. Likewise, widespread species demonstrated more negative water potentials at turgor loss, more negative saturated osmotic potential, lower symplastic water fraction and higher bulk modulus of elasticity values. Turgor loss point (TLP) and bulk modulus of elasticity were the best predictors of lethal water potential while symplastic water fraction and bulk modulus of elasticity were included as predictors of lethal RWC.

4. Inherent differences in physiological traits contributing to drought tolerance are associated with differences in tropical tree species distributions in relation to rainfall seasonality. These results, combined with lack of support for hypothesized historical factors, strongly implicate climate as a determinant of tree species distributions around the KPL.

Key-words: rainfall seasonality gradient, physiological adaptation, tropical rain forest, Malaysia, Thailand

Introduction

Water availability is often considered as one of the key factors limiting regional tree species distributions in lowland tropical forests (reviewed in Borchert 1998; Veenendaal & Swaine 1998) and correlative evidence in support of this relationship is ample (Condit 1998; Bongers *et al.* 1999; Oliveira & Fontes 2000; Pyke *et al.* 2001). Despite the importance of water availability to regional species distributions in the tropics, quantitative examinations of the mechanistic bases of these apparent relationships are rare (but see Tyree *et al.* 2003; Engelbrecht, Kursar & Tyree 2005; Engelbrecht *et al.* 2007a).

Species distributions along water availability gradients, whether local or regional, are potentially determined by differential resistance to drought due to physiological or morphological traits (Cao 2000; Tyree *et al.* 2002, 2003; Khurana & Singh 2004; Maherali, Pockman & Jackson 2004; Baltzer *et al.* 2005). These may be traits contributing to

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*Correspondence author. Biology Department, 63B York Street, Mount Allison University, Sackville, NB E4L 1G7, Canada. E-mail: jbaltzer@mta.ca

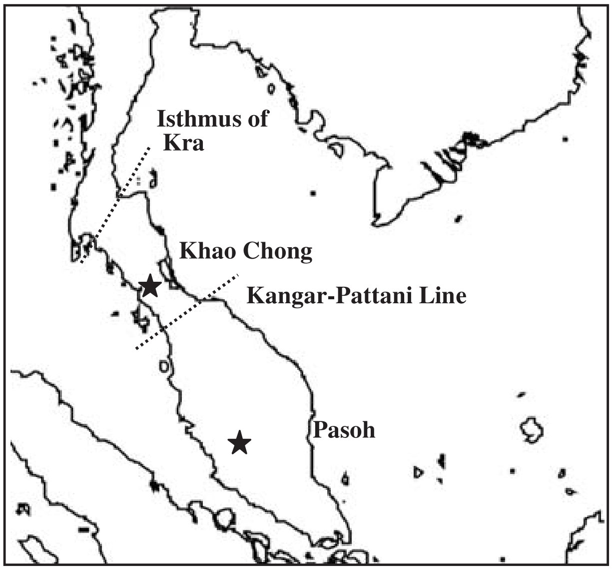

Fig. 1. Map of the locations of the Kangar–Pattani Line (KPL; dashed line), Isthmus of Kra, Pasoh Forest Reserve (Pasoh; Peninsular Malaysia, 2°58′ N, 102°18′ E) and Khao Chong Peninsular Botanical Garden (Khao Chong; Peninsular Thailand, 7°34′ N, 99°47′ E). The region to the north of the KPL has largely seasonal rainfall while the region to the south is primarily aseasonal.

drought tolerance (e.g. cell survival at low water potentials, decreased vulnerability of xylem vessels to embolism, osmotic adjustment) or delay (e.g. deeper rooting systems, early stomatal closure, low cuticular conductance) but will be extremely advantageous for survival and, potentially, continued growth during periods of water shortage (reviewed in Ludlow 1989; Bréda *et al.* 2006). Such adaptations should contribute to tree species distributions pan-tropically due to latitudinal gradients of rainfall seasonality in these regions. Likewise, drought resistance strategies may be particularly important for species inhabiting forests with severe or extended dry periods and may be of increasing relevance if El Niño related drought events increase in frequency and severity over time as predicted (e.g. Timmermann *et al.* 1999).

A well-recognized, but understudied, floristic and climatic transition, the Kangar–Pattani Line (KPL) (Van Steenis 1950a; Whitmore 1984), bisects the Malay–Thai Peninsula close to the Malaysian border (Fig. 1). Approximately 575 plant genera reach their distributional limits at this line (Van Steenis 1950). Both historical and environmental mechanisms have been invoked to explain this distributional pattern, but empirical support for either hypothesis is lacking. According to the historical explanations, past dispersal boundaries caused by ancient seaways during periods of high sea levels have led to current distributions (Woodruff 2003). Alternatively, the rapid turnover of species at the KPL may be due to a corresponding change in environmental conditions. The KPL marks the transition from aseasonal evergreen forests in the south (0 month of drought) to wet seasonal evergreen forests that experience 2–3 months of drought to the north with negligible change in total annual rainfall (Whitmore 1984; Ashton 1997). The close correspondence between species distributional limits and this rainfall seasonality transition has also been proposed as a primary mechanism maintaining species distributional limits with respect to the KPL (Whitmore 1984; Ashton 1995; Richards 1996). A recent study examining differences in adult tree performance as a function of distribution in relation to the KPL demonstrated that widespread species tend to have more conservative patterns of growth and are less responsive to local variation in edaphic factors when compared with species confined to the aseasonal forests (Baltzer *et al.* 2007). Such patterns support the hypothesized relationship between broad geographic ranges and greater tolerance of abiotic stress (Morin & Chuine 2006). However, the physiological mechanisms underlying these performance-related differences and, ultimately, species distributions have yet to be examined.

The capacity of plant tissue to withstand desiccation is considered a crucial determinant of drought tolerance (Ludlow 1989; Auge *et al.* 1998). Recent comparative work examining drought tolerance in Panamanian tree species has shown lethal leaf water potential and corresponding relative water contents (RWCs) to be excellent correlates of field-based drought performance (Tyree *et al.* 2002, 2003; Engelbrecht *et al.* 2005, Engelbrecht, Tyree & Kursar 2007b). Engelbrecht *et al.* (2005, 2007a) examined performance of saplings of co-occurring woody species using irrigated and rain-excluded plots and demonstrated a close correspondence between performance under drought, and both local and regional species distributions in relation to water availability. However, it is not clear what physiological traits underlie this variation in species ability to postpone dehydration and whether these more readily determined traits can likewise be used to predict species distributions in relation to rainfall.

Moisture-release curves describe the relationship between leaf water potential and leaf RWC, and are used to estimate a suite of physiological drought tolerance traits that may be expected to correspond with measures of desiccation tolerance described above (e.g. Flower & Ludlow 1986; see Table 1 for pressure–volume traits and their definitions). As leaf RWC decreases, turgor pressure also decreases, eventually reaching a point at which the cell wall is flaccid and cell water potential equals cell osmotic potential (turgor loss point, TLP; Table 1). With further drying, the leaf tissue will incur permanent damage, however, as water potential is determined both by solute and pressure potentials, elasticity of the cell wall, solute potential and/or partitioning of water between the apoplast and symplast can influence the TLP (Radin 1983; reviewed in Kozlowski & Pallardy 2002). These traits differ genetically among species and many species have the capacity to adjust these parameters in response to prolonged drought in order to avoid injury and/or maintain cell function during drought (mechanisms reviewed in Kozlowski & Pallardy 2002). An increased apoplastic water fraction may function as a reservoir which could act to buffer the symplasm against water loss (Joly & Zaerr 1987) and the maintenance of symplastic water volume contributes to cell turgor. Likewise, turgor loss can be

Table 1. Symbols, units of measurement and definitions for all traits measured in the study. Ψ_{lethal} and $\text{RWC}_{\text{lethal}}$ were determined using desiccation tolerance trials while the remaining traits were measured by constructing pressure–volume curves for well-watered individuals

Trait	Symbol	Units	Definition
Lethal water potential	Ψ_{lethal}	MPa	Lowest leaf water potential associated with living leaf tissue
Lethal relative water content	$\text{RWC}_{\text{lethal}}$	%	Lowest leaf relative water content associated with living leaf tissue
Turgor loss point	TLP	MPa	The water potential at which turgor pressure is zero; the cell wall is flaccid and cell water potential equals osmotic potential
Solute potential at full turgor	$\Psi_{\pi s}$	MPa	A component of leaf water potential determined by the solute concentration/accumulation within the cells at saturation
Bulk modulus of elasticity from full turgor to turgor loss	$\varepsilon_{\text{max-TLP}}$	MPa	The slope of the change in turgor pressure with changing relative water content providing a measure of the elasticity of the cell wall
Maximum symplastic water fraction	W_s	%	A measure of the proportion of the leaf water content contained within the cells (symplastically)

postponed via increased solute concentration which results in a reduction in solute potential or via reduced cell wall elasticity. Lower cell wall elasticity causes a faster drop in water potential for a given reduction in RWC by increasing tension in the cell; both result in a decrease in tissue water potential at a given RWC and thus a steeper soil–leaf water potential gradient allowing for maintenance of turgor to more negative tissue water potentials than in species not employing these strategies.

In the present study, following methods developed by Tyree *et al.* (2002, 2003) combined with an examination of plant water relations using pressure–volume analysis, we test whether tree species that have widespread distributions and can occur under conditions of seasonal drought show systematic differences in drought tolerance traits when compared with species that are confined to wetter, aseasonal areas. If species ability to tolerate water shortage is contributing to distributions, then species occurring in the seasonally dry forests should: (i) maintain living tissue at lower water contents and potentials; and (ii) exhibit water relations parameters corresponding to a drought tolerance strategy (more negative TLP and osmotic potential at saturation, lower symplastic water fraction and higher bulk modulus of elasticity; see Table 1 for definitions) when compared with species restricted to the aseasonal forests. If, however, species distributions were primarily determined by historical dispersal barriers (e.g. ancient seaways) and continue to be maintained by slow dispersal then systematic differences in drought tolerance-related traits would not be expected. Understanding the mechanisms underlying tropical tree species distributions in relation to water availability is crucial, particularly in light of the predicted changes in patterns of precipitation in tropical regions. This study is one of the first to test how drought tolerance and the underlying physiological traits contribute to the regional distribution patterns of tropical tree species.

Methods

PLANT MATERIAL AND DISTRIBUTIONS

We collected mature seeds of 24 tree species (Table 2) from July to October 2005 in the Pasoh Forest Reserve (2°58′ N, 102°18′ E) and the Khao Chong Peninsular Botanical Garden (7°34′ N, 99°47′ E) (hereafter Pasoh and Khao Chong; Fig. 1). The average rainfall at Pasoh and Khao Chong are 1950 mm year^{-1} (0 month of drought) and 2700 mm year^{-1} (2–3 months of drought), respectively. Seeds of two or more individuals were obtained for each species with the exception of two (Table 2). As often as was possible, we obtained seeds of congeneric species pairs differing in geographic distribution or from both Khao Chong and Pasoh for species occurring in both locations; as a consequence the numbers of adults available as seed sources was sometimes low (e.g. if the only available fruiting congener had few fruiting adults). The use of congeneric species pairs is desirable as it allows for the comparison of traits of interest between two groups independent of phylogenetic signal (Harvey & Pagel 1991). In this study, we conducted phylogenetically controlled analyses as well as analyses that did not correct for phylogeny as there were many unpaired study species.

We classified each species as widespread, southern or northern based on its distribution with respect to the KPL. The ranges were based on plant taxonomic records. Primary sources were the *Tree Flora of Malaya* (Whitmore 1972), *Flora Malesiana* (Van Steenis 1950b) and *Flora of Thailand* (Smitinand & Larsen 1970), all of which list the states/provinces and other countries in which the species occurs. Additional range data were collected from other reliable sources (Symington 2004; Van Welzen & Chayamarit 2005).

Seeds were germinated and seedlings grown in polybags (15·2 cm diameter × 22·9 cm height) filled with clay-rich soil collected near Pasoh. All seedlings were grown in shade structures covered in neutral density shade cloth providing 15% full sunlight. Maximum/minimum temperature and humidity were 23/31 °C and 62/100%, respectively. Microenvironmental measurements were made using Hobo Weather Stations (Onset Instruments, Bourne, MA). Ten blocks with 2–5 replicates per species were arranged in the nursery. Block and seedling positions on benches were rotated regularly to avoid confounding effects of light and temperature gradients. Until we initiated desiccation treatments seedlings were hand watered every evening if diurnal rainfall had not been sufficient.

DESICCATION TOLERANCE TRIALS

In September 2006, we constructed a rainout shelter made of transparent plastic sheeting in the nursery. After shelter construction, all seedlings were watered thoroughly following which water was withheld from eight blocks while two blocks were maintained as controls and hand-watered on a daily basis. Between 30 and 40 individuals per species were included in this portion of the study.

Table 2. List of study species, family and distributions, Dist. (N, Northern, S, Southern, W, Widespread) in relation to the Kangar–Pattani Line

Family	Species	Abb.	Dist.	Location
Dipterocarpaceae	*Parashorea stellata* Kurz.	Pt	N	KC (5)
	Parashorea densiflora (Y.Sl.) ex Sym.	Pd	S	P (1)
	Shorea guiso (Blanco) Blume	Sg	W	P (2)
	Shorea lepidota (Korth) Blume	Sl	S	P (> 3)
	Shorea macroptera Dyer	Sm	S	P (> 3)
	Shorea parvifolia Dyer	Sp	S	P (> 3)
	Vatica bella v. Slooten	Vb	S	P (3)
	Vatica odorata (Griff.) Symington	Vo	W	KC (2)
Euphorbiaceae	*Mallotus penangensis* Müll. Arg.	Mp	S	P (3)
	Neoscortechenia kingii Hk.f.	Nk	S	P (2)
Fabaceae	*Millettia atropurpurea* (Wall.) Benth.	Ma	W	P (2); KC (5)
	Sindora coriacea (Baker) Prain	Sc	W	P (3); KC (2)
	Sindora wallichii Graham ex Benth	Sw	S	P (3)
Fagaceae	*Lithocarpus wrayii* (King) A. Lamus	Lw	S	P (2)
	Quercus semiserrata Roxb.	Qs	N	KC (2)
Irvingaceae	*Irvingia malayana* Oliv. ex. Benth	Im	W	KC (2)
Phyllanthaceae	*Aporosa globifera* Hook f.	Ag	S	P (2)
	Aporosa microstachya Hook f.	Am	W	P (5)
	Aporosa symplocoides (Hook f.) paqx	As	S	P (3)
Polygalaceae	*Xanthophyllum affine* Korth.	Xa	W	P (1)
Sapotaceae	*Palaquium maingayi* K&G	Pm	S	P (3)
	Palaquium sumatrana Burck,	Ps	W	KC (2)
	Payena lucida (Don) DC	Pl	W	P (> 3)
Violaceae	*Rinorea anguifera* (Lour.) OK	Ra	W	P (8)

Abbreviations (Abb.) correspond to those in Figs 2 and 3. Location indicates the seed collection site (P, Pasoh, KC, Khao Chong); number of seed sources is indicated in parentheses. In the Dipterocarpaceae, mast fruiting often did not allow accurate counts of seed sources thus the numbers represent the seed collection locations.

Table 3. Description of the visual wilt states used to characterize plants during the desiccation tolerance trials

Wilt state	Visual symptoms
Normal	No signs of wilting
Slightly wilted	Slight leaf angle changes with no other noticeable changes to the laminar tissue
Wilted	Substantial leaf angle change; often protruding leaf veins; no necrotic laminar tissue
Severely wilted	Severe leaf angle change and leaf vein protrusion; necrotic patches, particularly at leaf margins
Nearly dead	Most leaves necrotic with some newer leaves maintaining live tissue near the midrib

Seedling height at the experimental onset varied substantially among species from 17·3 ± 0·9 cm (mean ± SE; *Parashorea densiflora*) to 58·0 ± 2·9 cm (*Milletia atropurpurea*, Malay provenance) although seedling age only ranged from 10 to 14 months. Due to these size differences we decided that examining the time course of drought responses would not be meaningful, as it would be largely influenced by variation in seedling size and resulting variation in the rate of soil drying. We measured water potential and RWC of plants at five wilting stages following Tyree *et al.* (2002, 2003): normal (control), slightly-wilted, wilted, severely-wilted and nearly-dead (Table 3). All measurements were made between 12.00 and 16.00 h when water stress will be maximized. At each wilting stage measured individuals were photographed and detailed notes were taken on the state of the plant. A number of species failed to show any signs of wilting for several weeks after initiation of the desiccation treatment; therefore, periodic water potential and RWC measurements were made for comparison with control values to ensure that these species were not experiencing drought stress without visual symptoms, though this was never the case. At each wilting stage, at least five individuals were randomly selected across blocks avoiding previously measured individuals. A single leaf (fully-expanded, near the apex) was removed from each plant and weighed to 0·001 g immediately before water potential measurement. We measured water potential using a pressure chamber (Model 1000, PMS Instruments, Corvallis, OR), following which leaves were dried at 70 °C for 48 h.

For all species, tissue water potential and RWC decreased with wilt stage (Supplementary Fig. S1). However, as our primary interest was the assessment of species differences in desiccation tolerance, we used water potentials and RWCs corresponding to wilt stage 4 (nearly-dead) in the analyses presented here. This measure of desiccation tolerance corresponds closely with seedling performance under drought conditions in the field (Tyree *et al.* 2003; Engelbrecht *et al.* 2007b) and represents the lowest water potential and RWC values associated with living leaf tissue (Ludlow 1989; Auge *et al.* 1998) (i.e. further decreases would result in plant death). These traits will thus be denoted hereafter as Ψ_{lethal} and $\text{RWC}_{\text{lethal}}$, respectively (Table 1). Low germination success and consequently insufficient replicates of *Vatica bella* and *V. odorata* prohibited their inclusion in the desiccation tolerance trials.

PRESSURE–VOLUME MEASUREMENTS

Moisture release curves describe the reduction in leaf water potential with decreasing leaf RWC (Tyree & Hammel 1972). We constructed moisture release curves for at least three individuals per species from the control blocks. Such measurements made under well-watered conditions allow for the assessment of genetically-based differences in water relations parameters (reviewed in Kozlowski & Pallardy 2002). It should be noted, however, that due to the relatively low numbers of seed sources that maternal effects cannot be discounted. For each curve, at least 15 cm of the shoot was cut, immediately immersed in water and recut. Cut stems were immersed in tap water for 2–3 h, wrapped in plastic film and re-immersed for 12 h in the dark at room temperature. Tissue rehydration is necessary in order to ensure that all samples are near saturation thus allowing for construction of the entire moisture release curve.

Following rehydration, we constructed moisture release curves for single leaves. We followed the free transpiration method (e.g. Hinckley *et al.* 1980; Lenz, Wright & Westoby 2006). For each sample, a single, fully expanded, healthy leaf was cut from the sample, gently surface dried and weighed to 0·001 g before and after measurement of water potential. The average of these two measurements was used to calculate RWC. During each reading the chamber was pressurized with compressed air and depressurized very slowly (at $< 0{\cdot}01$ MPa s^{-1}). Samples were left to dry on the bench between measurements made at fixed intervals. The following traits were estimated from the resulting pressure–volume curves (plot of inverse water potential vs. RWC): TLP, solute potential at full turgor ($\Psi_{\pi s}$), symplastic water fraction (W_s) and bulk modulus of elasticity ($\varepsilon_{\text{max-TLP}}$). Trait definitions and units of measurement can be found in Table 1. We obtained estimates of TLP, $\Psi_{\pi s}$ and W_s using least squares linear regression fit to the linear portion of the pressure–volume curves following Schulte & Hinckley (1985). Specifically, extrapolating the linear portion of the plot to the ordinate and abscissa provide estimates of $\Psi_{\pi s}$ and W_s, respectively. Calculation of $\varepsilon_{\text{max-TLP}}$ followed Lenz *et al.* (2006). Correction for over-rehydration followed from Kubiske & Abrams (1990). Reliable pressure–volume measurements were not obtained for six species (*Payena lucida*, *Palaquium maingayi*, *P. sumatrana*, *Sindora coriacea*, *S. walichii* and *Lithocarpus wrayii*) due to technical difficulties.

ANALYSIS

We examined variation in measured traits using nested analysis of variance (predictor variables: distribution, species nested within distribution). Due to the limited number of species with northern distributions, we employed a binary distribution variable depending on the species' occurrence above the KPL. Specifically, we classified all species whose distributions included the seasonally dry forests to the north of the KPL as widespread and those restricted to the aseasonal forests south of the KPL as southern. To examine phylogenetically corrected group differences in measured traits between congeneric/confamilial pairs, we used nested ANOVAS with two predictor variables: genus and distribution nested within genus. Specifically, seven species pairs were included in these analyses: *Aporosa*, *Lithocarpus*/*Quercus*, *Palaquium*, *Parashorea*, *Shorea*, *Sindora* and *Vatica*. For reasons outlined above, the *Palaquium*, *Lithocarpus*/*Quercus* and *Sindora* pairs could not be measured for pressure–volume traits while the *Vatica* pair could not be included in measurement of Ψ_{lethal} or $\text{RWC}_{\text{lethal}}$.

Ψ_{lethal} quantifies the minimum water potential associated with living tissue and corresponds with drought performance in the field (Tyree *et al.* 2003) making it a very ecologically meaningful variable. We therefore focus on assessing which of the pressure–volume parameters may be contributing most to interspecific and distributional differences in this key parameter. To do this we employed two methods. First, analysis of covariance (ANCOVA) was used to examine the relationships of the measured traits to Ψ_{lethal} and examine potential shifts in these relationships as a function of distribution. Second, multiple regression analyses were performed for the 17 species for which all traits were measured in order to quantify which traits contribute most to Ψ_{lethal} and $\text{RWC}_{\text{lethal}}$ (the two key drought tolerance-related traits according to Tyree *et al.* 2003). Predictor variables included TLP, $\Psi_{\pi s}$, $\varepsilon_{\text{max-TLP}}$ and W_s. Model selection was based on the minimum AIC. Lower AIC values indicate a more parsimonious model (Burnham & Anderson 1998), therefore, ΔAIC values were calculated for model selection.

Pairwise trait correlations were quantified using type II regression using the (S)MATR program (Falster, Warton & Wright 2003). In order to examine how measured traits were associated and assess where the two species groups were located in this multivariate trait space, we conducted a principal components analysis (PCA). As all traits were not measured for every species (see explanation above) this analysis was limited to 17 species (note that two provenances of *M. atropurpurea* were included in this analysis). With the exception of the type II regression, all analyses were conducted using R (R v. 2·1; The R Foundation for Statistical Computing, Vienna, Austria).

Results

DO DIFFERENCES IN DROUGHT TOLERANCE TRAITS CORRESPOND WITH SPECIES DISTRIBUTION?

Substantial distribution-related differences among species' physiological traits corresponded to drought tolerance strategies. With respect to the pressure–volume traits, species displayed a nearly twofold range in mean TLP (Fig. 2). Despite this large variation in mean TLP, the widespread species (i.e. species whose distributions include the seasonally dry forests north of the KPL) showed more negative TLPs than species restricted to the aseasonal forests south of the KPL (Fig. 2). Solute potential at full turgor ($\Psi_{\pi s}$) was likewise more negative in the widespread than the southern species (Fig. 2) indicating greater solute concentration at full turgor. Cell wall elasticity ($\varepsilon_{\text{max-TLP}}$) was greater in widespread than southern species, indicating more rigid cell walls in the former. Maximum symplastic water fraction (W_s) was lower in widespread than southern species (Fig. 2). In addition to the distribution-related differences in pressure–volume traits, significant differences existed in both tissue water potentials and RWCs in nearly-dead plants between the two distributional categories (Fig. 2). Specifically, widespread species maintained living tissue at more negative water potentials (Ψ_{lethal}) than did southern species. Likewise, $\text{RWC}_{\text{lethal}}$ was lower in widespread than southern species, indicating that species occupying areas that experience regular seasonal drought are able to maintain living tissue under greater water stress and at lower RWC than are species restricted to forests having aseasonal rainfall.

All patterns described for both pressure–volume and desiccation tolerance traits held when phylogeny was accounted for through intra-generic comparisons with the exception of

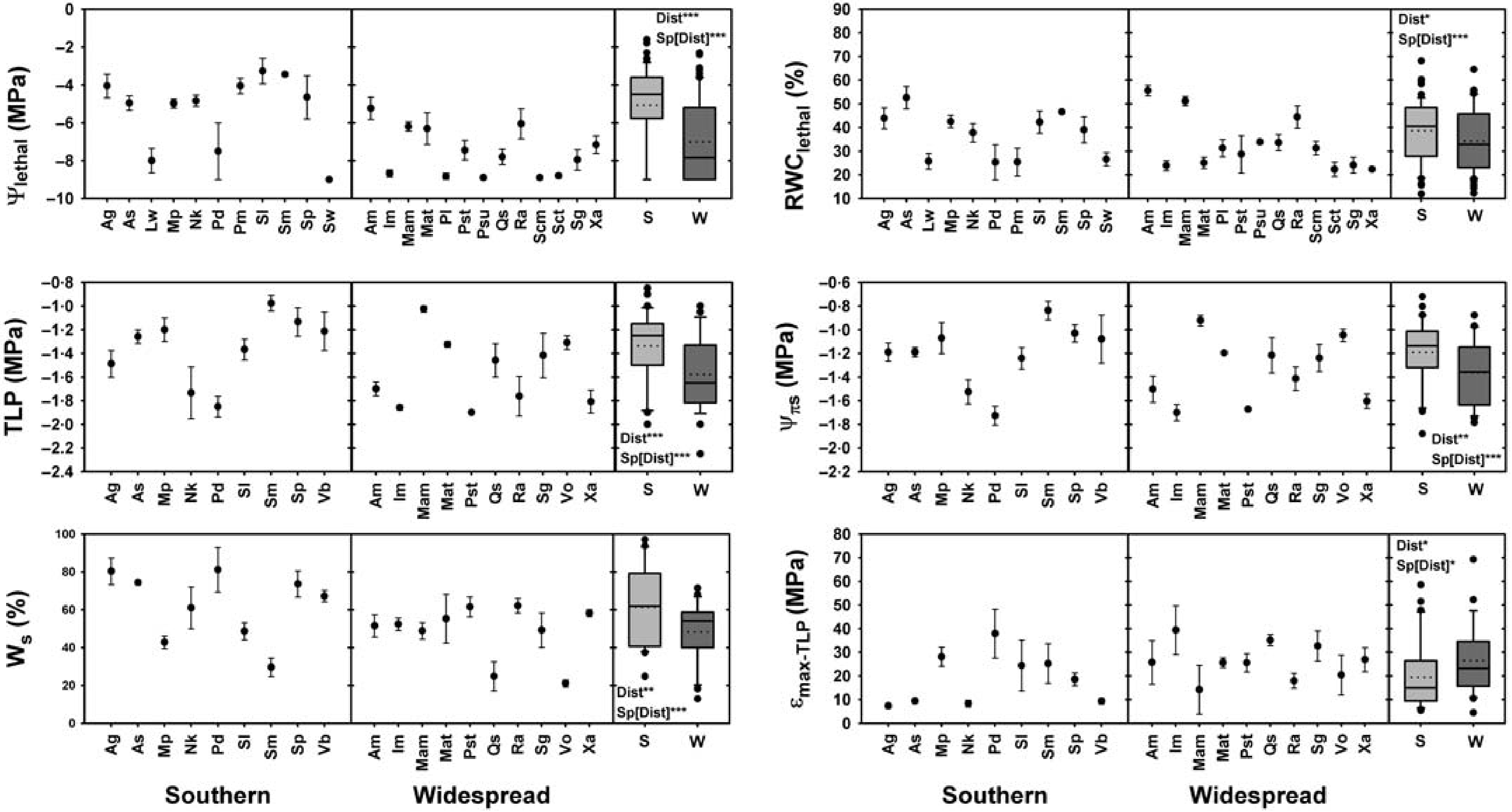

Fig. 2. Species mean (± SE) values for all measured traits divided based upon distribution in relation to the Kangar–Pattani Line (KPL). Southern species are those species whose distributions are restricted to the aseasonal forests south of the KPL while widespread species are all species with distributions including the seasonally dry forests north of the KPL. Trait names and definitions corresponding to the abbreviations can be found in Table 1. Species names corresponding to the abbreviations on the X-axis can be found in Table 2. Where two provenances were collected (*Milletia atropurpurea* and *Sindora coriacea*) the provenance is given by t (Thailand) or m (Malaysia) adjacent to the species code. Box plots contain pooled mean values by distribution (S, southern; W, widespread). Nested ANOVA (Dist, Distribution; Sp[Dist], species nested within distribution) results for each trait are provided with asterisks corresponding to P-values ($^{\cdot}P < 0{\cdot}1$, $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}0001$; NS, not significant). All analyses were conducted on log-transformed variables.

Table 4. Nested ANOVA results for paired congeneric or confamilial taxa

Trait	Genus	Distribution [Genus]
TLP	$11{\cdot}21_{3,30}$ (0·05)***	$3{\cdot}32_{4,30}$ (0·02)*
$\Psi_{\pi s}$	$15{\cdot}12_{3,30}$ (0·05)***	$3{\cdot}43_{4,30}$ (0·02)*
W_s	$6{\cdot}41_{3,30}$ (0·43)**	$3{\cdot}30_{4,30}$ (0·29)*
$\varepsilon_{max-TLP}$	$2{\cdot}72_{3,30}$ (0·55)	$1{\cdot}21_{4,30}$ (0·33)
Ψ_{lethal}	$18{\cdot}22_{5,62}$ (1·24)***	$7{\cdot}93_{6,62}$ (0·65)***
RWC_{lethal}	$12{\cdot}39_{5,62}$ (0·06)***	$2{\cdot}98_{6,62}$ (0·02)*

Seven pairs were included in the analysis (*Parashorea*, *Shorea*, *Vatica*, *Sindora*, *Lithocarpus*/*Quercus*, *Aporosa* and *Palaquium*); however, the *Palaquium*, *Lithocarpus*/*Quercus* and *Sindora* pairs could not measured for pressure–volume traits while the *Vatica* pair could not be included in measurement of Ψ_{lethal} or RWC_{lethal} (reasons for exclusion are outlined in Methods). For each trait the *F*-value (SS) is given. Adjacent asterisks correspond to *P*-values ($*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}0001$, values without designation are not significant). All analyses were conducted on log-transformed variables.

the differences in $\varepsilon_{max-TLP}$ (Table 4). It is worthwhile to note that certain species displayed trait values not corresponding well with the distributional patterns (Fig. 2). Specifically, southern-distributed *L. wrayi*, *Neoscortechenii kingii*, *P. densiflora* and *S. walichii* all behaved more similarly to widespread species in some desiccation tolerance-related traits (Fig. 2). Of the widespread species, *Aporosa microstachya*, the Malaysian provenance of *M. atropurpurea* and *Rinorea anguifera* showed aberrant values for some of the measured traits (Fig. 2).

TRAIT ASSOCIATIONS

A PCA was conducted to assess how the measured drought tolerance traits are associated with one another and whether species with differing distributions segregated in multivariate trait space. The first and second components explained 55% and 27% of the variation, respectively (Fig. 3), and were the only two significant components. Overall, species segregated nicely into distributional categories. On the right hand of the first axis are species having high values of Ψ_{lethal}, $\Psi_{\pi s}$ and TLP, and low values of RWC_{lethal}. With the exception of *P. densiflora*, this group consisted entirely of species occurring in seasonally dry forests (widespread species) (Fig. 3). The Malay provenance of *M. atropurpurea* was grouped in this analysis with the southern species located on the left hand side of the first axis. Distributional groupings also segregated, though to a lesser extent, along the second axis with widespread species tending toward the lower half of the second axis with higher values of $\varepsilon_{max-TLP}$ and lower W_s values (Fig. 3).

DETERMINANTS OF LETHAL WATER POTENTIAL

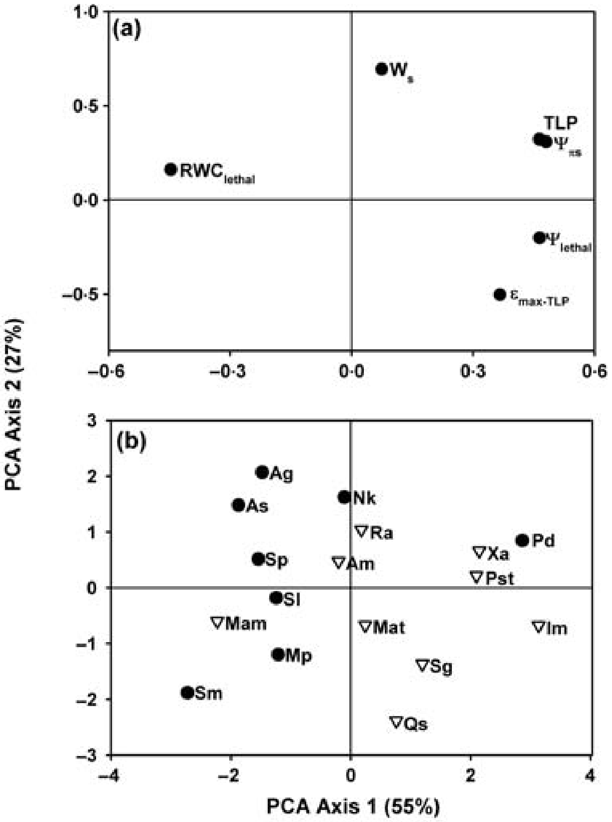

Fig. 3. Principal components analysis of six seedling traits of 17 tropical tree species. (a) Loading plot for the first two components; (b) Species loadings on the first two axes. Species abbreviations are given in Table 2. Species restricted to aseasonal forests south of the KPL (southern) are denoted by filled circles while species whose distributions include seasonally dry forests to the north of the KPL (widespread) are indicated with open triangles. Trait abbreviations, definitions and units can be found in Table 1.

Table 5. Coefficients of determination for type II regression relationships among pairs of measured traits

	Ψ_{lethal}	RWC_{lethal}	TLP	$\Psi_{\pi s}$	$\varepsilon_{max-TLP}$
RWC_{lethal}	0·39**	–	–	–	–
TLP	0·29*	0·23	–	–	–
$\Psi_{\pi s}$	0·32*	0·27*	0·94***	–	–
$\varepsilon_{max-TLP}$	0·40**	0·37**	0·11	0·15	–
W_s	0·00	0·00	0·09	0·14	0·12

Trait definitions, abbreviations and units of measurement can be found in Table 1. Statistical significance: $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}0001$; values without designation are not significant.

Type II regression analyses show significant relationships of Ψ_{lethal} and RWC_{lethal} to all variables except W_s. The relationship between TLP and $\Psi_{\pi s}$ was the strongest of all measured correlations (Table 5). ANCOVA similarly determined that all of the measured traits aside from W_s were significant linear predictors of Ψ_{lethal} (Fig. 4). Not surprisingly, as these traits were measured in concert, RWC_{lethal} showed the strongest relationship with Ψ_{lethal}. In all five relationships, species distribution resulted in significant downward shifts in the

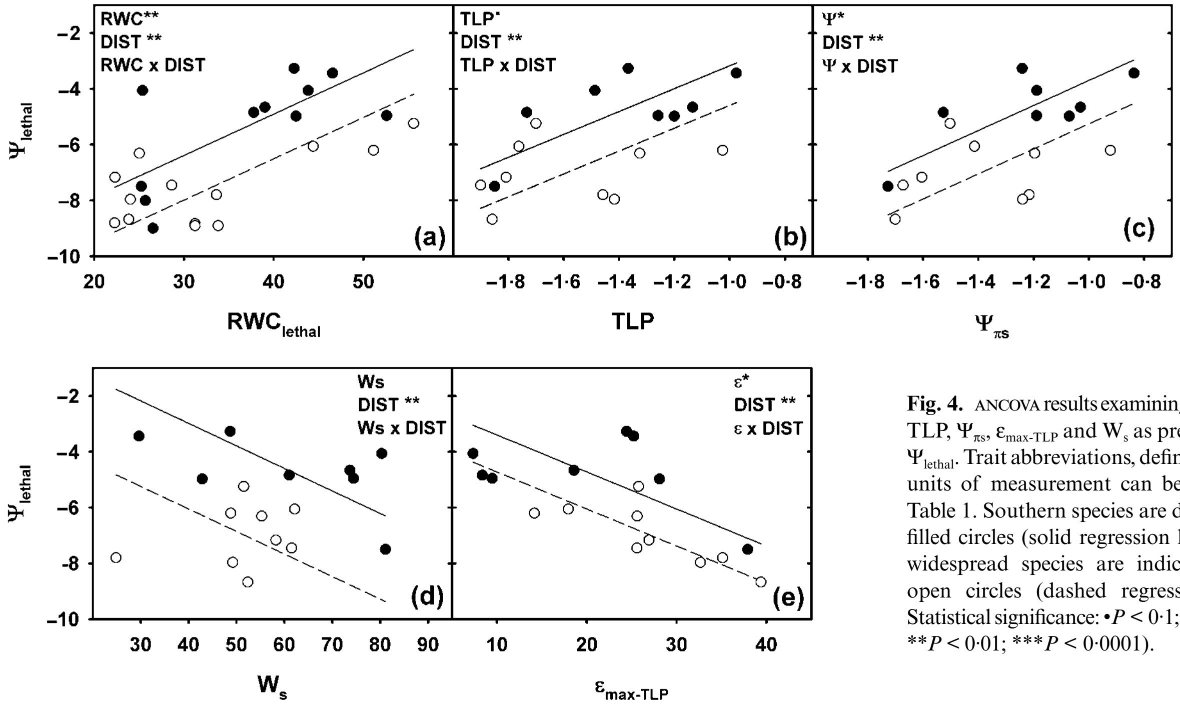

Fig. 4. ANCOVA results examining $\text{RWC}_{\text{lethal}}$, TLP, $\Psi_{\pi s}$, $\varepsilon_{\text{max-TLP}}$ and W_s as predictors of Ψ_{lethal}. Trait abbreviations, definitions and units of measurement can be found in Table 1. Southern species are denoted by filled circles (solid regression line) while widespread species are indicated with open circles (dashed regression line). Statistical significance: •$P < 0·1$; *$P < 0·05$; **$P < 0·01$; ***$P < 0·0001$).

Table 6. Minimum AIC-selected multiple regression model examining physiological water relation traits as predictors of (a) Ψ_{lethal} and (b) $\text{RWC}_{\text{lethal}}$

(a) Model $r^2 = 0·54$; $F_{2,14} = 8·35$; $P = 0·0041$

Variable	Parameter estimate	SE	*t*-value	Pr > |*t*|
Intercept	−0·72	1·50	−0·480	0·6389
TLP	2·10	1·01	2·075	0·0569
$\varepsilon_{\text{max-TLP}}$	−0·09	0·03	−2·773	0·0150

(b) Model $r^2 = 0·48$; $F_{2,14} = 6·37$; $P = 0·0108$

Variable	Parameter estimate	SE	*t*-value	Pr > |*t*|
Intercept	−71·36	11·93	5·982	< 0·0001
W_s	−0·25	0·15	−1·668	0·1176
$\varepsilon_{\text{max-TLP}}$	−0·84	0·24	−3·561	0·0031

Predictors included TLP, W_s, $\Psi_{\pi s}$ and $\varepsilon_{\text{max-TLP}}$. Trait definitions, abbreviations and units of measurement can be found in Table 1.

intercepts (Fig. 4); although it is appealing to look for adaptive explanations for such shifts, a more likely explanation given that downward shifts occurred every trait comparison is that this finding is an artefact of the striking differences in Ψ_{lethal} among southern and widespread species, providing further evidence of the importance of this key trait in tree species distributions in relation to rainfall seasonality (Fig. 2). We will therefore not discuss these findings further.

To further examine which traits were contributing most to differences in Ψ_{lethal} and $\text{RWC}_{\text{lethal}}$, we performed multiple regression analyses to examine the contribution of the pressure–volume traits to these variables. The minimum AIC selected models from these two analyses retained TLP and $\varepsilon_{\text{max-TLP}}$ as predictors of Ψ_{lethal}, while $\varepsilon_{\text{max-TLP}}$ and W_s were retained as predictors of $\text{RWC}_{\text{lethal}}$ (Table 6).

Discussion

Seasonal drought has been shown to influence seedling survival in dry, moist and wet tropical forests (Turner 1990; Green & Newbery 2002; Marod *et al.* 2002; Poorter & Hayashida-Oliver 2002; Engelbrecht *et al.* 2005, 2007a). Determining the mechanisms contributing to species' differential drought responses is therefore crucial in understanding the factors that limit tree species distributions in these biologically rich areas. The primary aim of the present study was to assess whether a mechanistic basis exists for the hypothesized relationship between tree species distributions and the shift from aseasonal to seasonal rainfall moving northward along the Malay–Thai Peninsula. Our results from a common garden study demonstrate the existence of inherent differences in species' physiological traits contributing to drought tolerance between species that occur in the seasonally dry forests compared with those restricted to the aseasonal forests. If differences in seasonality of rainfall were not influencing species distributions, such systematic trait differences would not be expected. This study demonstrates a physiological basis for regional tree species distributions with respect to rainfall seasonality (see also Tyree *et al.* 2003; Engelbrecht *et al.* 2005) and has important implications for tropical forest dynamics and community composition with predicted hydrological and climatic changes (Hulme & Viner 1998; IPCC 2001).

DROUGHT TOLERANCE TRAITS AS PREDICTORS OF SPECIES DISTRIBUTIONS AT THE KPL

In the present study, species occupying seasonally dry forests to the north of the KPL exhibited a number of traits characteristic of a drought tolerance strategy. These species had inherently more negative water potentials at turgor loss (TLP). Loss of leaf turgor is the first stage of wilting and corresponds roughly with the water potential at which stomates are closing or closed (Brodribb *et al.* 2003). Maintenance of TLP at more negative water potentials should thus allow for continued carbon gain to lower soil and tissue water potentials. Although photosynthetic capacity is reduced during drought, some species maintain reasonably high rates even under severe drought conditions (e.g. Slot & Poorter 2007); undoubtedly maintenance of cell turgor plays an integral role in this. Widespread species also had the capacity to maintain living tissue at significantly more negative leaf water potentials (Ψ_{lethal}) and lower RWCs ($\text{RWC}_{\text{lethal}}$). These findings corroborate recent studies in Panama showing that these two traits correspond closely both with species distribution along a rainfall gradient and species response to drought in the field (Tyree *et al.* 2003; Engelbrecht *et al.* 2007a). Widespread species also maintained more negative osmotic potential at full turgor ($\Psi_{\pi s}$), lower cell wall elasticity (greater $\varepsilon_{\text{max-TLP}}$) and lower maximum symplastic water fraction (W_s). Higher values of the elasticity modulus have been linked with greater foliar tissue density (thicker cell walls and lower proportional intercellular air spaces) (Niklas 1991a,b; Niinemets 2001) typically found in species occupying drier environments (Niinemets 2001). Similarly, at low tissue elasticity (high $\varepsilon_{\text{max-TLP}}$), water potential changes more with a given change in tissue water content (rigid tissues more quickly result in negative pressure potentials within the cell). This results in larger soil–leaf water potential gradients and consequently greater water uptake from the drying soil at a given water content than a species with high elasticity (Bowman & Roberts 1985). The findings of more negative $\Psi_{\pi s}$ and higher $\varepsilon_{\text{max-TLP}}$ are, however, highly auto-correlated with respect to plant function as both traits have the potential to contribute to TLP (reviewed in Kozlowski & Pallardy 2002). A more negative $\Psi_{\pi s}$ will reduce the TLP as solute potential contributes directly to tissue water potential while greater values of $\varepsilon_{\text{max-TLP}}$ correspond with lower flexibility of cell walls to symplastic water loss resulting in a more rapid drop in water potential at a given RWC due to increase tension within the cell and acting to lower the water potential at turgor loss. A strong positive relationship existed between TLP and $\Psi_{\pi s}$ whereas the relationships between TLP and either $\varepsilon_{\text{max-TLP}}$ or W_s were not significant (Table 5). This suggests that differences in $\Psi_{\pi s}$ may be having a greater influence on TLP in the tree species in question; however, both $\Psi_{\pi s}$ and $\varepsilon_{\text{max-TLP}}$ were maintained as highly significant predictors of TLP in a multiple regression analysis with minimum AIC selection criteria (ΔAIC to the next best model was 11·13; $\varepsilon_{\text{max-TLP}}$ $P < 0{\cdot}0001$, $\Psi_{\pi s}$ $P < 0{\cdot}0001$; W_s was not retained in this model). Niinemets (2001) similarly suggested that moderate changes in leaf osmotic potential combined with elasticity adjustments might allow plants to cope with severe or prolonged water stress. These physiological differences, apparent even when phylogeny was accounted for, could contribute to both growth and survival during seasonal droughts and potentially increase long-term performance of the widespread vs. southern species in seasonally dry forests such as those found north of the KPL (J.L. Baltzer *et al.* unpublished data). It should be noted, however, that the strongest distribution-related signal in the data was apparent in Ψ_{lethal}, a finding suggestive of greater importance of survival-related traits in species distributions.

Recent work by Engelbrecht *et al.* (2007b) points toward Ψ_{lethal} and $\text{RWC}_{\text{lethal}}$ as the primary correlates of tropical tree species distributions in relation to gradients of rainfall availability. Although our data highlight strong responses of both traits to species distribution in relation to rainfall seasonality, our PCA results indicate that in addition to these two variables, both TLP and $\Psi_{\pi s}$ are also key traits for distinguishing between distributional groups, which segregated most strongly across the first axis (Fig. 3). Likewise, Poorter & Markesteijn (in press) demonstrate that a range of traits relating to resource capture, dry matter content and drought deciduousness differentiate between moist and dry forest species in Bolivia. Although Poorter & Markesteijn (in press) did not examine Ψ_{lethal} or $\text{RWC}_{\text{lethal}}$ as determinants of species distribution, their findings combined with those of the present study suggest that there is a suite of underlying traits correlated with drought tolerance and species distribution with respect to rainfall. Further, our multiple regression analyses highlight that more readily quantified pressure–volume traits are reasonable predictors of both Ψ_{lethal} and $\text{RWC}_{\text{lethal}}$, with bulk modulus of elasticity playing a prominent role as a predictor of both traits (Table 6).

One caveat to the above conclusions is that changes in pressure–volume traits for plants experiencing water deficit were not examined. Thus our conclusions are based solely on inherent differences in pressure–volume parameters under favourable conditions. Water relation parameters obtained from pressure–volume curves may vary with soil water conditions (e.g. Tyree & Jarvis 1982); however, species rankings have been shown to remain constant across soil water availabilities (e.g. Tschaplinski, Gebre & Shirsac 1998). Furthermore, there was close correspondence between pressure–volume traits and leaf water potentials in nearly dead plants. We therefore anticipate that our conclusions with respect to these traits are robust.

MECHANISMS CONTRIBUTING TO SPECIES DISTRIBUTIONS

Two potential locations exist where seaways could have bisected the Malay–Thai Peninsula during periods of high sea levels: the Isthmus of Kra (the narrowest portion of the peninsula south of the mainland) and the approximate location of the KPL (Fig. 1; Woodruff 2003). These locations correspond with two of the most important biogeographical transitions in this region. Seaways occurring at these locations multiple times should have resulted in strong genetic differentiation as well as dramatic species compositional shifts. Evidence for the existence of the hypothetical seaway at the Isthmus of Kra has been found. For example, deBruyn *et al.* (2005) examined genetic differentiation in populations of the freshwater crustacean *Macrobrachium rosenbergii* along the Peninsula and found a sharp genetic break between populations to the north and south of the Isthmus of Kra, providing evidence of the proposed northern seaway; no corresponding genetic break was detected around the KPL. Further phylogenetic analysis in other groups is needed to confirm this result. Likewise, while evidence of both floral and faunal transitions at the Isthmus of Kra is ample (Corbet 1941; Corbett & Hill 1992; Ridder-Numan 1998; Inger & Voris 2001; Hughes, Round & Woodruff 2003), there is little evidence of a faunal transition at the KPL (e.g. Hughes *et al.* 2003).

The second main hypothesis regarding determinants of species distributions along the Malay–Thai Peninsula is climatically based. The transition from aseasonal rainfall south of the KPL to a seasonally dry climate to the north has been linked repeatedly but qualitatively with the corresponding floristic transition (Whitmore 1984; Ashton 1995; Richards 1996). Under this hypothesis we predict differences in species' physiology- and growth-related traits corresponding to adaptations beneficial to differing distributions in this region. The data presented here provide strong support for this prediction. Specifically, drought tolerance-related physiological differences were evident between species restricted to the south of the KPL and those whose distributions include the seasonally dry forests north of the KPL. In a corresponding study, Baltzer *et al.* (2007) demonstrate that tree species with widespread distributions show more conservative patterns of growth and responsiveness to variation in local edaphic conditions when compared with southern species; a finding in keeping with the hypothesis that widespread species have greater tolerance to climatic variability and abiotic stress (cf. Morin & Chuine 2006). Combined, these results strongly support the role of rainfall seasonality in the current distributions of tree species in relation to the KPL. Similar work has yet to be conducted at the Isthmus of Kra.

Species distributions in this region are undoubtedly a function of a number of factors and further work is needed from both ecological and historical perspectives, if we are to fully understand the fascinating biogeographical patterns in this region. Continued efforts to understand these distributional patterns are crucial given the climatic changes predicted to occur under global change (e.g. Hulme & Viner 1998). Similar physiological mechanisms to those documented in the present study have been linked both with field performance under drought as well as local and regional tree species distributions in relation to water availability in Panama (Engelbrecht *et al.* 2005, 2007a). Combined, these data suggest that differential sensitivity to water availability is a key factor driving regional tropical tree species distributions.

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References

Ashton, P.S. (1995) Towards a regional forest classification for the humid tropics of Asia. *Vegetation Science in Forestry* (eds E.O. Box, R.K. Peet, T. Masuzawa, T. Yamada, K. Fujiwara & P.F. Maycock), pp. 453–464. Kluwer Academic Publishers, Amsterdam.

Ashton, P.S. (1997) South Asian evergreen forests: some thoughts toward biogeographic reevaluation. *Tropical Ecology*, **38**, 171–180.

Auge, R.M., Duan, X.G., Croker, J.L., Witte, W.T. & Green, C.D. (1998) Foliar dehydration tolerance of twelve deciduous tree species. *Journal of Experimental Botany*, **49**, 753–759.

Baltzer, J.L., Davies, S.J., Kassim, A.R., Noor, N.S. & LaFrankie, J.V. (2007) Geographic distributions in tropical trees: can geographic range predict performance and habitat association in co-occurring tree species? *Journal of Biogeography*, **34**, 1916–1926.

Baltzer, J.L., Thomas, S.C., Nilus, R. & Burslem, D.F.R.P. (2005) Edaphic specialization in tropical trees: physiological correlates and responses to reciprocal transplantation. *Ecology*, **86**, 3063–3077.

Bongers, F., Poorter, L., Van Rompaey, R.S.A.R. & Parren, M.P.E. (1999) Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. *Journal of Vegetation Science*, **10**, 371–382.

Borchert, R. (1998) Responses of tropical trees to rainfall seasonality and its long-term changes. *Climate Change*, **39**, 381–393.

Bowman, W.D. & Roberts, S.W. (1985) Seasonal changes in tissue elasticity in chaparral shrubs. *Physiologia Plantarum*, **65**, 233–236.

Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006) Temperate forest trees and stands under severe drought: review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.

Brodribb, T.J., Holbrook, N.M., Edwards, E.J. & Gutierrez, M.V. (2003) Relationship between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell and Environment*, **26**, 443–450.

Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: A Practical Information Theoretic Approach*. Springer-Verlag, New York.

Cao, K.F. (2000) Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *Journal of Tropical Ecology*, **16**, 101–116.

Condit, R. (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climate Change*, **39**, 413–427.

Corbet, A.S. (1941) The distribution of butterflies in the Malay Peninsula. *Proceedings of the Royal Entomological Society of London A*, **16**, 101–116.

Corbett, G.B. & Hill, J.E. (1992) *The Mammals of the Indomalayan Region: A Systematic Review*. Oxford University Press, Oxford, UK.

deBruyn, M., Nugroho, E., Hossain, M.M., Wilson, J.C. & Mather, P.B. (2005) Phylogeographic evidence for the existence of an ancient biogeographic barrier: the Isthmus of Kra Seaway. *Heredity*, **94**, 370–378.

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007a) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–83.

Engelbrecht, B.M.J., Kursar, T.A. & Tyree, M.T. (2005) Drought effects on seedling survival in a tropical moist forest. *Trees-Structure and Function*, **19**, 312–321.

Engelbrecht, B.M.J., Tyree, M.T. & Kursar, T.A. (2007b) Visual assessment of wilting as a measure of leaf water potential and seedling drought survival. *Journal of Tropical Forest Ecology*, **23**, 497–500.

Falster, D.S., Warton, D. & Wright, I. (2003) *(S)MATR: Standardised Major Axis Tests and Routines.* <http://www.bio.mq.edu.au/ecology/SMATR>.

Flower, D.J. & Ludlow, M.M. (1986) Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeonpea (*Cajanus cajan* (L.) millsp.) leaves. *Plant, Cell and Environment*, **9**, 33–40.

Green, J.J. & Newbery, D.M. (2002) Reproductive investment and seedling survival of the mast-fruiting tree, *Microberlinia bisulcata* A. chev. *Plant Ecology*, **162**, 169–183.

Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, New York.

Hinckley, T.M., Duhme, F., Hinckley, A.R. & Richter, H. (1980) Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity. *Plant Cell and Environment*, **3**, 131–140.

Hughes, J.B., Round, P.D. & Woodruff, D.S. (2003) The Indochinese–Sundaic faunal transition at the Ithsmus of Kra: an analysis of resident forest bird species distributions. *Journal of Biogeography*, **30**, 569–580.

Hulme, M. & Viner, D. (1998) A climate change scenario for the tropics. *Climate Change*, **39**, 145–176.

Inger, R.F. & Voris, H.K. (2001) The biogeographical relations of the frogs and snakes of Sundaland. *Journal of Biogeography*, **28**, 863–891.

IPCC (2001) *Climate Change 2001: Synthesis Report*. Intergovernmental Panel on Climate Change 3rd Assessment report. Cambridge University Press, Cambridge, UK.

Joly, J.J. & Zaerr, J.B. (1987) Alteration of cell-wall water content and elasticity in Douglas-fir during periods of water deficit. *Plant Physiology*, **83**, 418–442.

Khurana, E. & Singh, J.S. (2004) Germination and seedling growth of five tree species from tropical dry forest in relation to water stress: impact of seed size. *Journal of Tropical Ecology*, **20**, 385–396.

Kozlowski, T.T. & Pallardy, S.G. (2002) Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review*, **68**, 270–334.

Kubiske, M.E. & Abrams, M.D. (1990) Pressure–volume relationships in non-rehydrated tissue at various water deficits. *Plant Cell and Environment*, **13**, 995–1000.

Lenz, T.I., Wright, I.J. & Westoby, M. (2006) Interrelations among pressure–volume curve traits across species and water availability gradients. *Physiologia Plantarum*, **127**, 423–433.

Ludlow, M.M. (1989) Strategies in response to water stress. *Structural and Functional Responses to Environmental Stresses: Water Shortage* (eds. H.K. Kreeb, H. Richter & T.M. Hinckley), pp. 269–281. SPB Academic Press, The Hague, Netherlands.

Maherali, H., Pockman, W.T. & Jackson, R.B. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184–2199.

Marod, D., Kutintara, U., Tanaka, H. & Nakashizuka, T. (2002) The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology*, **161**, 41–57.

Morin, X. & Chuine, I. (2006) Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters*, **9**, 185–195.

Niinemets, U. (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, **82**, 453–469.

Niklas, K.J. (1991a) Biomechanical attributes of the leaves of pine species. *Annals of Botany*, **68**, 253–262.

Niklas, K.J. (1991b) Biomechanical responses of *Chamaedorea* and *Spathiphyllum* petioles to tissue dehydration. *Annals of Botany*, **67**, 67–76.

Oliveira, A.T. & Fontes, M.A.L. (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica*, **32**, 793–810.

Poorter, L. & Hayashida-Oliver, Y. (2002) Effects of seasonal drought on gap and understory seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, **16**, 481–498.

Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, **12**, 553–566.

Radin, R.W. (1983) Physiological consequences of cellular water deficits: osmotic adjustment. *Limitation to Efficient Water Use in Crop Production* (eds. H.M. Taylor, W.R. Jordan & T.R. Sinclair), pp. 267–276. ASA-CSSA-SSSA, Madison.

Richards, P.W. (1996) *The Tropical Rain Forest: An Ecological Study*, 2nd edn. Cambridge University Press, Cambridge, UK.

Ridder-Numan, J.W.A. (1998) Historical biogeography of *Spatholobus* (Leguminosae-Papillionoideae) and allies in SE Asia. *Biogeography and Geological Evolution of Southeast Asia* (eds. R. Hall & J.D. Halloway), pp. 259–277. Backhuys, Leiden, the Netherlands.

Schulte, P.J. & Hinckley, T.M. (1985) A comparison of pressure–volume curve data analysis techniques. *Journal of Experimental Biology*, **36**, 1590–1602.

Slot, M. & Poorter, L. (2007) Diversity of tropical tree seedling responses to drought. *Biotropica*, **39**, 683–690.

Smitinand, T. & Larsen, K. (1970) *Flora of Thailand*. Forest Herbarium, Royal Forest Department. Applied Scientific Research Corporation of Thailand, Bangkok.

Symington, C.F. (2004) *Forester's Manual of Dipterocarps* (revised by P.S. Ashton & S. Appanah; ed. by H.S. Barlow). Malayan Forest Records. Syonan-Hakubutukan, Kuala Lumpur, Malaysia.

Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694–697.

Tschaplinski, T.J., Gebre, G.M. & Shirsac, T.L. (1998) Osmotic potential of several hardwood species as affected by manipulation of throughfall precipitation in an upland oak forest during a dry year. *Tree Physiology*, **18**, 291–298.

Turner, I.M. (1990) Tree seedling survivorship and growth of 3 *Shorea* species in a Malaysian tropical rain forest. *Journal of Tropical Ecology*, **9**, 469–478.

Tyree, M.T. & Hammel, H.T. (1972) The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany*, **23**, 267–282.

Tyree, M.T. & Jarvis, P.G. (1982) Water in tissues and cells. *Encyclopedia of Plant Physiology, Physiological Plant Ecology II* (eds O.L. Lange, P.L. Nobel & C.B. Osmond), pp. 35–77. Springer, Berlin, Heidelberg, New York.

Tyree, M.T., Engelbrecht, B.M.J., Vargas, G. & Kursar, T.A. (2003) Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiology*, **132**, 1439–1447.

Tyree, M.T., Vargas, G., Engelbrecht, B.M.J. & Kursar, T.A. (2002) Drought until death do us part: a case study of the desiccation-tolerance of a tropical moist forest seedling-tree, *Licania platypus* (Hemsl.) Fritsch. *Journal of Experimental Botany*, **53**, 2239–2247.

Van Steenis, C.G.G.J. (1950a) The delimitation of Malesia and its main plant geographical divisions. *Flora Malesiana*, **1**, 1xx–1xxv.

Van Steenis, C.G.G.J. (1950b) *Flora Malesiana*. Series I: Spermatophyta. Koenigstein, West Germany.

Van Welzen, P.C. & Chayamarit, K. (2005) *Flora of Thailand Euphorbiaceae*. Nationaal Herbarium Nederland and Forest Herbarium, National Park, Wildlife and Plant Conservation Department, Bangkok. <www.nationaalherbarium.nl/thaieuph>.

Veenendaal, E.M. & Swaine, M.D. (1998) Limits to tree species distribution in lowland tropical rainforests. *Dynamics of Tropical Forest Communities* (eds D.M. Newbery, H.H.T. Prins & N. Brown), pp. 163–191. 37th Symposium of the British Ecological Society. Blackwell Science, Oxford.

Whitmore, T.C. (1972) *Tree Flora of Malaya: A Manual for Foresters*. Malayan Forest Records No. 26 (Forest Research Institute of Malaysia). Longman Malaysia, Kuala Lumpur, Malaysia.

Whitmore, T.C. (1984) *Tropical Rainforests of the Far East*, 2nd edn. Oxford University Press, Oxford, UK.

Woodruff, D.S. (2003) Neogene marine transgressions, palaeogeography and biogeographic transitions on the Thai–Malay Peninsula. *Journal of Biogeography*, **30**, 551–567.

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Supplementary material

The following supplementary material is available for this article:

Fig. S1. Species water potential and relative water content values for all measured wilting stages.

This material is available as part of the online article from: http://www/blackwell-synergy.com/do/full/10.1111/j.1365-2435.2007.01374.x
(This link will take you to the article abstract).