



# Sapwood density underlies xylem hydraulics and stored carbohydrates across 13 deciduous tree species in a seasonally dry tropical forest in Thailand

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## Abstract

**Key message** Sapwood density is coordinated with hydraulic capacity and non-structural carbohydrate reserves in xylem in the seasonally dry tropical forests.

**Abstract** Sapwood density (WD) is one characteristic underlying the divergence in life history strategies among species in seasonally dry tropical forests (SDTFs) since WD is linked to xylem hydraulic properties through its correlations with vessel anatomy, maximum photosynthetic capacity, and leaf phenology. However, it remains unclear how differences in WD contribute to the divergence in water conduction and non-structural carbohydrate (NSC) reserves during the dry season, the physiologically most severe period for woody plants. We hypothesized that heavy-wooded species maintain water conduction, photosynthesis, and translocation of carbon which result in high NSC reserves in xylem during the dry season. Using 13 deciduous tree species from a SDTF located in Northeast Thailand, we investigated the variation in WD and bark morphology in relation to hydraulic properties and NSC concentrations in xylem during the late-dry season. Percentage loss of conductivity (PLC) varied as a quadric function of WD: high PLC was observed in light- and heavy-wooded species. The maximum conductivity was not related to WD. The PLC was negatively related to the concentrations of soluble sugars and NSC in the trunk xylem, and these relationships underlined the negative association between WD and NSCs. We also found that species with thick bark showed relatively low PLC, and that dense-barked species exhibited higher NSC concentrations in branch xylem, but their linkages were generally weaker than WD. These results demonstrate that species hydraulics and NSC reserves are coordinated in SDTFs during the dry season, and that WD underlies these divergences.

**Keywords** Bark density · Xylem embolism · Hydraulic efficiency · Non-structural carbohydrates (NSC) · Seasonally dry tropical forest · Sapwood density

## Introduction

Seasonally dry tropical forests (SDTFs) account for nearly 42% of tropical forests around the world (Murphy and Lugo 1986), and are characterized by the seasonal variations

in resource availability, particularly in water. SDTFs are generally composed by diverse species with contrasting traits (phenological, physiological, and morphological characteristics) (Sterck et al. 2011; Méndez-Alonzo et al. 2013). Thus, SDTFs have provided opportunities to study how species with different traits cope with seasonal drought (e.g., Kitajima et al. 1997; Brodribb et al. 2002; Ishida et al. 2010). So far, studies have revealed that species' responses to seasonal drought can be summarized by several traits that have proximal influences on carbon and water use strategies (e.g., acquisition and processing).

Sapwood density (WD) is a key trait defining where species in SDTFs occur along a spectrum of strategies for carbon gain and desiccation resistance, thus influencing life history strategies (Chave et al. 2009; Sterck et al. 2011; Méndez-Alonzo et al. 2012). Light wood is often associated

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with high maximum hydraulic conductivity through having large vessels and maximum photosynthetic rate, which leads to high growth rates during the wet growing season (Santiago et al. 2004; Meinzer et al. 2008; Méndez-Alonzo et al. 2012; Hoeber et al. 2014). Such high conductivity, together with large water storage capacity (hydraulic capacitance) and stomatal closure at early desiccating conditions, prevents the drop in xylem water potential against drought, thus linking the low WD species to desiccation avoidance strategies (Bucci et al. 2004; Meinzer et al. 2008). In contrast, heavy wood is often associated with desiccation tolerance strategies such as increased resistance to drought-induced xylem embolism through enhanced implosion resistance of vessels (Hacke et al. 2001; Jacobsen et al. 2005; Pratt et al. 2007; Markesteijn et al. 2011; Fu et al. 2012; Janssen et al. 2020). Consequently, heavy-wooded species can maintain hydraulic integrity among organs under desiccating conditions and are thus more likely to survive during severe drought than light-wooded species (Slik 2004; Nardini et al. 2013; Greenwood et al. 2017; Aleixo et al. 2019). In addition, WD is often associated with leaf phenology; species with high WD tend to retain leaves longer as the dry period progresses, whereas species with low WD often shed leaves earlier at the beginning of the dry season (Méndez-Alonzo et al. 2012; Chen et al. 2021).

Although the linkages between WD and drought responses in xylem hydraulics have been well documented, it remains unclear how non-structural carbohydrate (NSC) reserves, another important physiological parameters that influence the metabolism, survival, and growth of trees, vary depending on species WD. SDTF trees face seasonal decoupling between carbon demand and supply due to the resource limitations (e.g., drought); thus, NSC reserves are important for buffering such asynchronies (Chapin et al. 1990; Hartmann and Trumbore 2016). In particular, branch and stem xylem constitutes nearly 80% of the total NSC pool in SDTF trees (Würth et al. 2005) and contributes to the survival and recovery of trees during long-lasting drought (McDowell et al. 2008; O'Brien et al. 2014; Kannenberg et al. 2018; Trugman et al. 2018; Nakamura et al. 2021). As discussed above, heavy-wooded species are expected to maintain photosynthetic carbon gain for longer during the dry season through high cavitation resistance and longer leaf retention time. Therefore, assuming that metabolic demands (e.g., growth and maintenance) are similar among species, it is expected that heavy-wooded species show a more positive carbon balance during drought, which means relatively high xylem NSC concentrations (McDowell et al. 2008, 2011), particularly in the late dry season than light-wooded species that would deplete xylem-stored NSC relatively fast during drought. We further expect that such positive WD–NSC relationship is tighter for organs far from the sources (e.g., trunk) than those close to them (e.g., distal branch) because

translocation of carbon from source to sink organs requires NSC gradient and tissue hydration (hydrostatic pressure) (e.g., Sala et al. 2010; Dannoura et al. 2019). Heavy-wooded species are expected to maintain relatively high NSC concentrations and leaf tissue hydration even in the dry season than light-wooded species, through sustained photosynthesis and xylem water conduction during the dry season. These characteristics of heavy-wooded species will contribute to the maintenance of active mobilization and translocation of soluble sugars from sources (i.e., leaves) to distal sinks, such as trunk and roots, resulting in relatively high level of NSC within sink tissues during the dry season.

A positive linkage between water transport and NSC concentrations is also expected from the role of NSC (particularly soluble sugars) in the maintenance of xylem hydraulic capacity (Salleo et al. 2004; Zwieniecki and Holbrook 2009; Yoshimura et al. 2016). Since most SDTF trees maintain xylem water transport capacity even in the driest period, despite large interspecific variations (Brodrribb et al. 2002; Ishida et al. 2010), xylem NSC may underpin this phenomenon. However, the role of NSC in xylem water transport has not been examined in SDTFs because most studies have focused on either NSCs or xylem hydraulics (e.g., Brodrribb et al. 2002; Würth et al. 2005; Ishida et al. 2010; Méndez-Alonzo et al. 2012; Signori-Müller et al. 2022).

In addition to WD, bark morphology may also influence xylem hydraulics and NSC via various mechanisms, such as buffering fluctuations in water potential, embolism refilling, stem photosynthesis, and possibly phloem transport capacity during the desiccating conditions (Salleo et al. 2004; Zwieniecki and Holbrook 2009; Rosell et al. 2014). Although the mechanistic linkages between bark morphology and xylem physiology are not completely understood, we examined the coordination between bark morphology (total bark density and thickness) and xylem hydraulics and NSC concentrations. Total bark density covaries with bark water content and possibly resistance to phloem transport against drought stress, as observed in xylem (e.g., Hacke et al. 2001) (e.g., Hacke et al. 2001), whereas bark thickness is associated with phloem conductive area and presence of stem photosynthesis among species (Rosell et al. 2014). Here, we focused on the branch as the influence of bark would be particularly large at the distal position where bark accounts for the greater volume and mass in stems (Rosell 2016).

In the present study, we examined the interspecific variation in sapwood density and bark morphology in relation to xylem water transport and NSC reserves in the driest period during the dry season, using 13 deciduous species from the SDTF in Northeast Thailand. Specifically, we measured the percentage loss of conductivity (PLC) and maximum hydraulic conductivity ( $K_{max}$ ) in branches as xylem water transport capacity and NSC concentrations in branches and trunks as xylem NSC reserves. We targeted

deciduous species to maximize interspecific variations in xylem hydraulic properties (Brodrribb et al. 2002; Chen et al. 2021). Specially, we tested the three hypotheses.

- 1) Species with higher WD and denser and thicker bark maintain xylem water transport capacity (low PLC and high  $K_{\max}$ ) even in the midst of dry season.
- 2) Species that maintain xylem water transport capacity have a positive carbon balance and high NSC concentrations in both branch and trunk xylem, because of prolonged carbon assimilation rates even in the dry season. This trend is stronger for trunk than branch, since long-distant transport of carbon requires higher NSC concentration gradients and hydration status in the leaves.
- 3) Reflecting (1) and (2), species with higher WD and denser and thicker bark have high NSC concentrations in both branch and trunk xylem, particularly in trunk, in the midst of dry season.

## Materials and methods

### Study site and plant species

This study was conducted at the Sakaerat Environmental Research Station (SERS) on the southwestern edge of the Khorat Plateau in Nakhon Ratchasima Province, Northeast Thailand (14°27'N–14°33'N, 101°51'E–101°57'E). Elevations of the SERS ranged from 250 to 765 m, with mean annual temperature of 25.3 °C and mean annual precipitation of 1107 mm (during 2006–2017, data available from <https://www.tistr.or.th/sakaerat/Meteorological>.

HTM). This site is characterized by a distinct dry season (< 30 mm/month in precipitation) that lasts for four months (from November–February). According to the Soil Map of the World (FAO/UNESCO 1974), the soil in this area is generally nutrient-poor and classified as Orthic Acrisols.

We selected 13 co-occurring and dominant tree species comprising seven families in SERS (Online Resource 1). Three to four healthy adult trees that received direct sunlight from the canopy were selected for each species. Most sampled trees were between 18 and 41 cm in DBH (diameter at breast height). All studied individuals were found in places with similar topographic conditions, and were at most 1.5 km apart. All tree species had the same growth forms (i.e., broad-leaved drought-deciduous trees) (Gardner et al. 2000). Plant nomenclature followed the World Flora Online (WFO 2021). A total of 12 xylem and bark traits were measured for each species (Table 1). Measurements and collection of xylem samples were conducted in February 2020, which corresponds to the driest period during the dry season when extractable soil water reaches nearly zero (Murata et al. 2012). Most trees started to shed their leaves during the mid-dry season (January–February) and had almost no leaves during the study period (K. Kawai, personal observation), similar to other SDTFs in Thailand (Elliott et al. 2006; Williams et al. 2008; Ishida et al. 2014).

### Xylem hydraulic properties

We measured the maximum xylem hydraulic conductivity ( $K_{\max}$ ) and percentage loss of conductivity (PLC) using one to three sunlit branches with fully developed bark for each tree from February 15–20, 2020. Using a 15 m-long pole

**Table 1** Xylem and bark traits, including minimum species mean, the mean of species mean, the maximum species mean, and standard deviation (SD) of species mean of 13 tree species at the Sakaerat Environmental Research Station in Northeast Thailand

Trait	Symbol	Unit	Mean (SD)	Min	Max	Species <sup>3</sup>
Maximum xylem-area-specific conductivity <sup>1</sup>	$K_{\max}$	kg m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup>	2.37 (1.58)	0.24	4.70	0.021
Percentage loss of conductivity <sup>2</sup>	PLC	%	54.2 (24.2)	10.4	84.9	<0.001
Mass-based soluble sugar concentration in the branch xylem	SS <sub>B</sub>	%	2.08 (0.74)	0.73	3.34	0.024
Mass-based starch concentration in the branch xylem	ST <sub>B</sub>	%	0.45 (0.34)	0.03	1.22	0.042
Mass-based concentration of soluble sugar and starch in the branch xylem	NSC <sub>B</sub>	%	2.52 (0.77)	1.07	3.73	0.046
Mass-based soluble sugar concentration in the trunk xylem	SS <sub>T</sub>	%	2.95 (1.42)	1.35	6.03	<0.001
Mass-based starch concentration in the trunk xylem	ST <sub>T</sub>	%	0.31 (0.20)	0.10	0.81	0.001
Mass-based concentration of soluble sugar and starch in the trunk xylem	NSC <sub>T</sub>	%	3.25 (1.42)	1.47	6.18	<0.001
Sapwood density	WD	g cm <sup>-3</sup>	0.54 (0.08)	0.36	0.62	<0.001
Total bark density	BD	g cm <sup>-3</sup>	0.52 (0.12)	0.34	0.78	<0.001
Total bark thickness <sup>1</sup>	BT	mm	1.42 (0.64)	0.53	2.68	<0.001

<sup>1</sup>Log<sub>10</sub>-transformed before analysis.

<sup>2</sup>Logit-transformed before analysis (for detail, see Materials and methods).

<sup>3</sup>Showing *P*-values for one-way ANOVA used to evaluate species differences.

For each species' trait data, see Online Resource 1.

pruner (Taketani Trading Co. Ltd., Osaka, Japan), branches were collected early in the morning (06:00–08:00) to avoid artificially-induced xylem embolism (Wheeler et al. 2013), and were immediately re-cut under water. Most of the branches were > 1 m in length to reduce the likelihood of open vessels being present. The branches were then immediately transported to the laboratory with the cut ends submerged in water, where they were enclosed in black plastic bags to relax the xylem tension. The branch xylem did not include the heartwood portion, which is typically regarded as a different color.

Using the method of Sperry et al. (1988), we measured hydraulic conductivity in the longest branch segments without any side branches. The length and diameter of all samples ranged from 5.5–43.0 cm with a mean value of 21.3 cm and from 2.2–6.4 mm with a mean value of 4.8 mm, respectively. After gently removing the bark at both ends, the branch sample was connected to the tubing system, and hydraulic pressure of approximately 5 kPa was applied to the end of the segments by placing the water bag containing 20 mM KCl solution to c. 50 cm height from the sample. The other end was connected to a plastic bottle on an electronic balance using a tube, and the water flow rate from the segment was measured. The water flow rate was divided by the pressure per unit length of the segment to obtain initial xylem hydraulic conductivity ( $K_{\text{initial}}$ ). Subsequently, the same segment was flushed with 20 mM KCl solution under 100 kPa for 15 min to remove air-induced xylem embolism, and the water-flow rate was measured again to yield the maximum xylem hydraulic conductivity ( $K_{\text{flushed}}$ ). The KCl solution was filtered through a 0.2  $\mu\text{m}$  pore diameter using a vacuum pump before the measurements. The PLC was calculated as follows:

$$\text{PLC} = \left( 1 - \frac{K_{\text{initial}}}{K_{\text{flushed}}} \right) \times 100 \quad (1)$$

After the measurements, the cross-sectional areas of the wood and pith at both ends were measured using a digital caliper, assuming a circular shape. The cross-sectional area of the xylem sapwood ( $A_s$ ) was obtained by subtracting the pith area from the wood area. The value of  $K_{\text{flushed}}$  was divided by  $A_s$  to obtain the maximum xylem-area-specific conductivity ( $K_{\text{max}}$ ). We excluded *Pterocarpus macrocarpus* from the analysis because copious amounts of latex produced by the xylem disabled the measurement of PLC and  $K_{\text{max}}$ . All the hydraulic measurements were performed at room temperature (approximately 30 °C) in our laboratory.

## Non-structural carbohydrate concentrations in branch and trunk xylem

The concentrations of soluble sugars and starch were quantified in different stem segments from those used to calculate PLC and  $K_{\text{max}}$  (however, the same branches) for 12 species (*Rothmannia wittii* was excluded). We also measured the concentrations of total NSC, assuming that it is the sum of soluble sugars and starch. In addition, we collected one stem core (3–4 cm in depth from the cambium) per individual tree from 13 species using an increment borer (5.15 mm in diameter; Haglöf, Långsele, Sweden) at 1.3 m height from February 14–21, 2020. As NSC concentrations vary with time of day, particularly in branch wood (Yoneda et al. 2002; Tixier et al. 2018), we standardized the sampling time to be early in the morning (06:00–08:00) and in the morning (9:30–11:30) for branch and trunk xylem, respectively. These stem cores did not include the heartwood portion, typically regarded as a different color.

After collecting the samples, they were immediately transported to the laboratory in a dark cooler box. Then, we swiftly measured sample dimensions of branch (see section the below) and trunk xylem, followed by the immediate removal of bark before oven-drying (65 °C, >72 h). After drying, the pith was removed for branch xylem and the remnants were ground to a fine powder using a mill, followed by extraction in 80% (v/v) ethanol three times. The supernatant was extracted via centrifugation and used to quantify the soluble sugar content using the phenol-sulfuric acid method (Dubois et al. 1951). The starch in the remaining pellets was depolymerized to glucose by amyloglucosidase, and its content was quantified using the mutarotase–glucose oxidase method (Glucose C-II test; Wako, Tokyo, Japan).

## Sapwood density and bark morphology

We measured the sapwood density and the density and thickness of total bark in branch, using the same branch segments for NSC measurements and additional segments from different branches (in total,  $n = 1\text{--}2$  per individual tree). First, we determined the fresh volume of the samples with and without bark by measuring the diameter and length of the sample, assuming a cylindrical shape, using a digital caliper. The total bark thickness (BT) was calculated as the average difference between the sample diameter with and without bark. Then, the xylem and bark samples were oven-dried (65 °C, > 72 h) and weighed. Branch wood density (WD) and total bark density (BD) were calculated as the dry mass of wood and bark divided by their fresh volume, respectively. Our measurements did not distinguish the inner bark, which is involved in phloem transport, from the outer bark because of the difficulty in visual classification. However, we considered that our values of total bark mainly reflected

those of inner bark based on its predominantly consolidation and on the positive correlations between inner- and total-bark density (Rosell et al. 2014) and between inner-bark and outer bark thickness among species (Rosell 2016).

## Statistical analysis

All analyses were performed using R (version 3.6.1; R Core Team 2019). We calculated the mean trait values for each species, and some trait values were transformed before analysis to improve the normality and homoscedasticity of the residuals in the regressions (Table 1). Traits ranging in  $(0, \infty)$  were  $\log_{10}$ -transformed. PLC which ranges in a limited range  $[0, 100]$  was first added minimum non-zero PLC values among samples (1.05%) and expressed in the proportional range  $[0, 1]$ , then logit-transformed as recommended by Warton and Hui (2011). We examined the hypothesized relationships among species using Pearson's product-moment correlation. When a significant correlation ( $P < 0.05$ ) was observed, the line was fitted using the standardized major axis using the R package 'smatr' (Warton et al. 2012). Species differences in traits were examined by one-way ANOVA.

## Results

The co-occurring 13 deciduous tree species in the SDTF in Thailand showed markedly different xylem traits, particularly starch concentration in branch ( $ST_B$ ), maximum xylem-specific conductivity ( $K_{max}$ ), percentage loss of conductivity (PLC), and total bark thickness (BT) (Table 1, Online Resource 1). The  $ST_B$  varied 38.2-fold (0.03–1.22%),  $K_{max}$  varied 19.6-fold (0.24–4.70  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ), PLC varied 8.2-fold (10.4–84.9%), and BT varied by 5.0-fold (0.53–2.68 mm) among species (all,  $P < 0.05$ ). Sapwood density showed 1.7-fold variation among species. Total bark density (BD) varied more than wood density (2.3- vs. 1.7-fold), with statistically similar mean values (paired  $t$ -test,  $P = 0.28$ ). BD and wood density were highly and positively correlated (Table 2). The BT was not significantly related to wood or bark density.

The concentrations of soluble sugars were, on average, 13.1-fold higher than that of starch in both branches and trunks (paired- $t$  test, both  $P < 0.001$ ). The soluble sugar concentration was, on average, 1.5-fold higher in the trunk than in the branch ( $P = 0.03$ ), whereas the concentrations of starch and NSC were not significantly different between them ( $P = 0.29$ ;  $P = 0.08$ , respectively, Online Resource 2). In addition, soluble sugar concentrations were not significantly related to starch concentrations in either the branch ( $P = 0.68$ ) or trunk ( $P = 0.85$ ).

**Table 2** Correlations between sapwood density and bark morphology for 13 tree species at the Sakaerat Environmental Research Station in Northeast Thailand

	WD	BD
BD	0.70 **	
BT <sup>1</sup>	-0.19 ns	-0.24 ns

<sup>1</sup>  $\log_{10}$ -transformed before analysis.

WD: sapwood density, BD: Total bark density, BT: Total bark thickness, ns: not significant

\*\* $P < 0.01$

## Sapwood density, bark morphology, and xylem hydraulics

Differently from Hypothesis 1, PLC was independent of wood density (WD,  $r = 0.06$ ,  $P = 0.85$ ). However, except for *Xylia xylocarpa* with the lowest PLC, we obtained the relationship represented by a quadric function with a downward convexity ( $R^2 = 0.54$ ,  $P = 0.05$ , all coefficients  $P < 0.05$ ,  $n = 11$ , Fig. 1a). WD was not correlated with maximum xylem-specific conductivity ( $K_{max}$ ,  $P = 0.49$ , Fig. 1d). Therefore, the native conductivity before removing the air-induced embolism was strongly and negatively correlated with PLC among species ( $r = -0.71$ ,  $P = 0.01$ , data not shown).

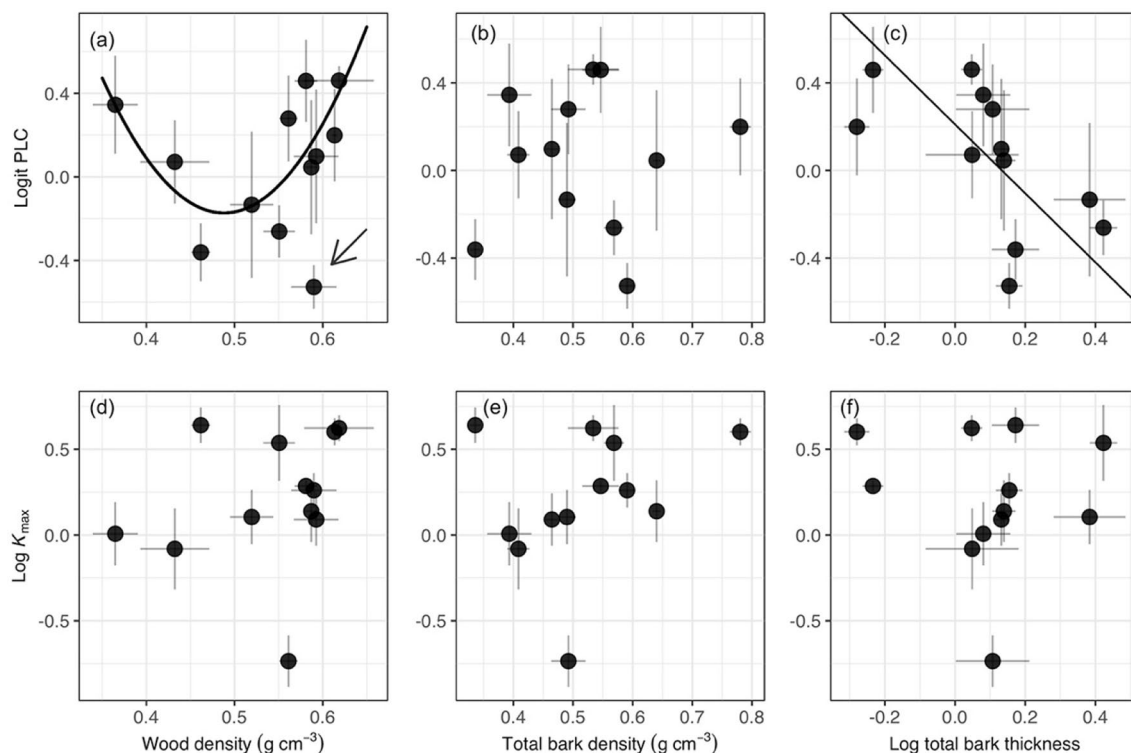
We also found that lower PLC was associated with thicker bark (Fig. 1c,  $r = -0.59$ ,  $P = 0.04$ ), but not with total bark density (Fig. 1b,  $r = 0.07$ ,  $P = 0.82$ ). Similar to wood, the bark traits were not related to  $K_{max}$  (Fig. 1e, f,  $P > 0.46$ ).

## Xylem hydraulics and NSC reserves

Consistent with our Hypothesis 2, high PLC was associated with low concentrations of soluble sugars and total NSC in the trunk, a distal sink from the source, and not in the branch, when excluding the species with the highest NSC (*Morinda coreia*, Fig. 2a, e). PLC was not related to starch concentrations in either the branch or trunk (Fig. 2c).  $K_{max}$  was not related to xylem NSC concentrations (Fig. 2b, d, f).

## Sapwood density, bark morphology, and NSC reserves

Contrary to our Hypothesis 3, dense wood and bark were not necessarily associated with high NSC concentrations (Fig. 3), except for a marginally-significant positive relationship between branch starch concentrations and WD ( $R^2 = 0.27$ ,  $P = 0.08$ , Fig. 3d). We found negative correlations between WD and the concentrations of soluble sugars ( $R^2 = 0.38$ ,  $P = 0.03$ , Fig. 3a) and NSC ( $R^2 = 0.43$ ,  $P = 0.02$ , Fig. 3g) in the trunk when removing the species with the lowest WD (*Canarium subulatum*). Dense bark was associated with low starch concentrations in the trunk (Fig. 3e) and



**Fig. 1** Relationships between xylem hydraulic properties and sapwood density and bark morphology for 12 tree species in a seasonally dry tropical forest in Northeast Thailand. The percentage loss of conductivity in the branch xylem (PLC) against (a) wood density, (b) total bark density, and (c) total bark thickness. Maximum xylem-area-specific conductivity ( $K_{\max}$ ) against (d) wood density,

(e) total bark density, and (f) total bark thickness. PLC was logit-transformed (unitless; see Materials and methods). Error bars represent 1 standard error (SE). The solid curves indicate significant relationship among traits, excluding the species with the lowest PLC (*Xylia xylocarpa*), denoted by a black arrow in (a). The line in (c) was fitted by the standardized major axis regression

high NSC concentrations in the branch (Fig. 3h), whereas bark thickness was not correlated with any index of xylem NSC concentrations (Fig. 3c, f, i).

## Discussion

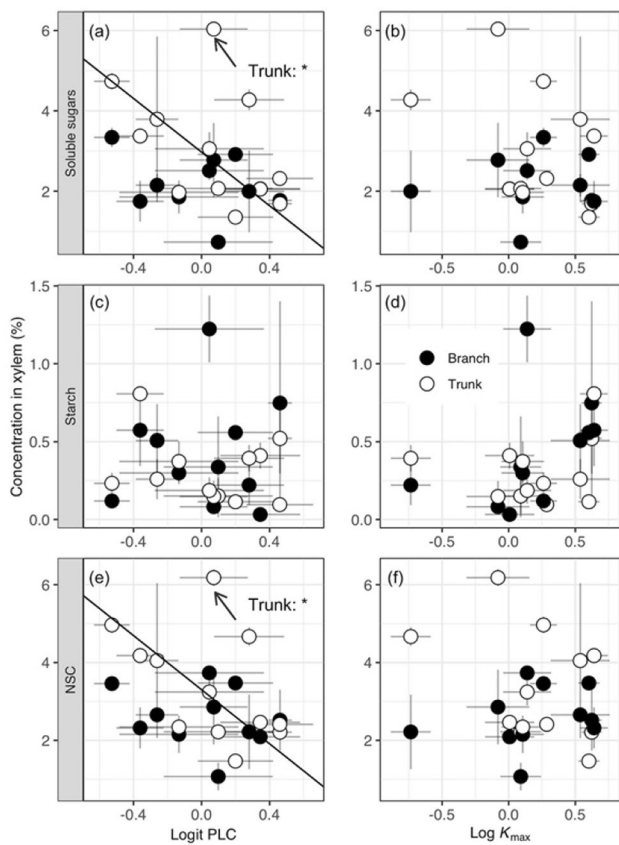
Sapwood density (WD) and bark morphology varied greatly among 13 deciduous tree species. Their variation was associated with species differences in xylem hydraulics and NSC reserves during the dry season in the SDTF in Northeast Thailand. We discuss the possible mechanisms underlying the observed relationships and their ecological implications.

### Coordination between sapwood density, bark morphology, and water transport

Heavy wood is often constituted of vessels with high implosion resistance, reflecting the positive correlation of lumen-to-wall ratios between fibers and vessels (Jacobsen et al. 2005). Thus, species with higher WD are usually associated with higher resistance to drought-induced

xylem embolism (Hacke et al. 2001; Jacobsen et al. 2005; Markesteijn et al. 2011; Janssen et al. 2020). We thus hypothesized that heavy-wooded species exhibit low degree of native embolism (low PLC) and high conductivity ( $K_{\max}$ ) during the late dry season. However, in the present study, the PLC did not vary linearly along the WD, but varied as a quadric function with a downward convexity (Fig. 1). As a result, higher PLC was observed in species with higher or lower WD. WD was not related to  $K_{\max}$  (Fig. 1d), showing that  $K_{\max}$  is strongly regulated by vessel features rather than WD (e.g., Lens et al. 2011).

The increased PLC for species with high WD seems counterintuitive, but may reflect that such woody plants have more negative water potential, due to their loose stomatal control and excess transpiration (Hoffmann et al. 2011), or to retaining a large leaf area under desiccating conditions (Méndez-Alonzo et al. 2012; Wolfe et al. 2016), or to preference for dry microhabitats. Positive correlations of WD with PLC or drought-induced branch dieback have been often observed during severe droughts in the temperate and tropical forests (Hoffmann et al. 2011; Chen et al. 2021), implying that species with high WD show narrow safety margins



**Fig. 2** Relationships between mass-based concentrations of soluble sugars, starch, and non-structural carbohydrates (NSC) in branch and trunk xylem with xylem hydraulic properties for 12 tree species in a seasonally dry tropical forest in Northeast Thailand. The concentration of soluble sugars against (a) percentage loss of conductivity at branch xylem (PLC) and (b) maximum xylem-area-specific conductivity ( $K_{\max}$ ). The concentration of starch against (c) PLC and (d)  $K_{\max}$ . The concentration of NSC (the sum of that of soluble sugars and starch) against (e) PLC and (f)  $K_{\max}$ . Black and white circles indicate values for branch and trunk, respectively. Error bars represent 1 standard error (SE). The solid lines indicate significant relationships among traits and were fitted by the standardized major axis regression. The solid lines in (a) and (e) indicate the trends excluding the species with the highest NSC (*Morinda coreia*), denoted by black arrows. Note that the scale is different for starch concentration. \* $P < 0.05$

for hydraulic failure. Branch dieback is frequently observed in trees even at the study site in SDTFs, including species with high WD (K. Kawai, personal observation).

Bark morphology can influence xylem water transport through its correlations with the hydraulic capacitance and xylem anatomy. We found that thicker bark was associated with lower PLC (Fig. 1c), suggesting that thick bark functions in water storage and alleviates increasing xylem tension under desiccating conditions (Rosell et al. 2014). Thus, thick bark can be viewed as a measure of desiccation avoidance strategies. Thick bark is often thought to provide high fire resistance by protecting the cambium against

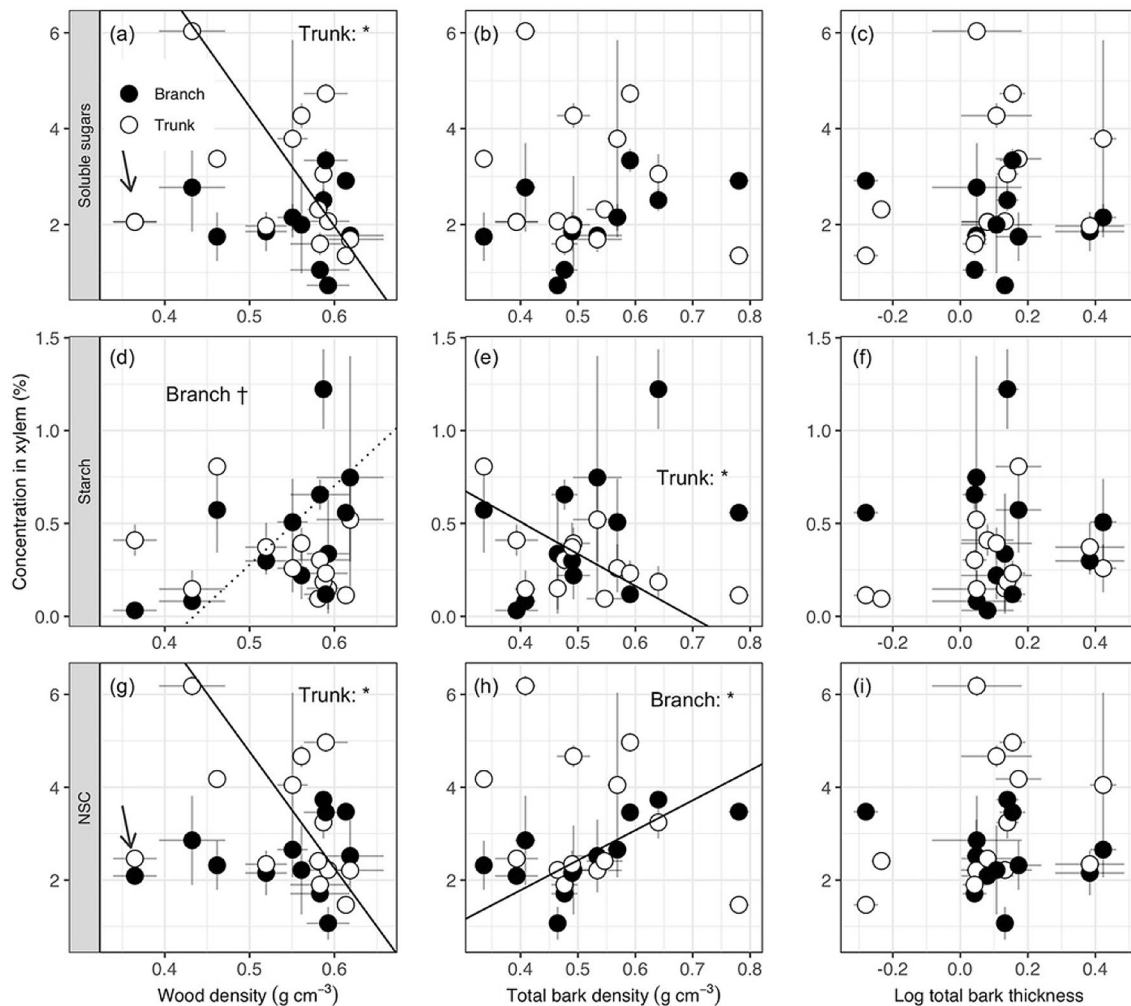
lethal temperatures during forest fires (Pinard and Huffman 1997; Hoffmann et al. 2003; Brando et al. 2012). Our results suggest that woody species with thick bark in SDTFs have increased fire resistance and drought resistance.

### Coordination of xylem water transport and NSC reserves

In the present study, the concentrations of soluble sugars (i.e., the easily usable form of NSCs for trees) were generally higher than those of starch. This phenomenon means that (1) tree growth ceases before photosynthesis (Kamo et al. 1995; McDowell et al. 2011; Nakai et al. 2018), and then soluble sugar concentrations increase and that (2) starch is converged to soluble sugars to maintain tree metabolisms (e.g., respiration, osmotic adjustment, and xylem refilling) (Muller et al. 2011; Fatichi et al. 2014; MacNeill et al. 2017; Signori-Muller et al. 2021; Signori-Müller et al. 2022).

Xylem hydraulics and NSC reserves determine the safety from hydraulic failure and carbon depletion, respectively, thus influencing drought survival of trees (McDowell et al. 2008; Anderegg et al. 2016; Trugman et al. 2018; Nakamura et al. 2021). The linkages and feedback processes between these two elements have been proposed (Sala et al. 2010; McDowell et al. 2011; Kono et al. 2019). However, the direct examination is still limited in the fields, particularly in SDTF trees. Consistent with Hypothesis 2 that xylem hydraulics capacity and NSCs reserves in xylem are positively coordinated, we revealed that species with low cavitation levels and higher native conductivity had relatively high NSCs within the trunk xylem (Fig. 2a, e). The similar phenomenon has been reported in subtropical trees (Yoshimura et al. 2016). There are at least two possible explanations for this phenomenon of trees. First, species that maintain water conduction would maintain photosynthesis and tissue hydration longer as the dry period progresses. Such species could maintain mobilization and translocation of carbon during the drought, leading to high NSC concentrations at the distal sinks (e.g., McDowell et al. 2008; McDowell et al. 2011). In contrast, species that reduce water transport capacity from roots to canopy and photosynthesis earlier in the dry season would lose capacity to translocate carbon and thus consume their NSC by respiration and osmoregulation, resulting in low NSC levels in the late dry season.

Second, it has recently been shown that soluble sugars within sapwood contribute to maintaining xylem hydraulic capacity by osmotically-driven water induction into embolized vessels via sugar deposition (Zwieniecki and Holbrook 2009), avoiding an increase in PLC. However, PLC was not significantly correlated with NSC in the branch (Fig. 2a, c, e). This decoupling may reflect that the branch NSC pool is small and sensitive to external and internal factors in the natural conditions (Newell et al.



**Fig. 3** Relationships between mass-based concentrations of soluble sugars, starch, and non-structural carbohydrates (NSC) in xylem with sapwood density and bark morphology for 13 tree species in a seasonally dry tropical forest in Northeast Thailand. The concentration of soluble sugars against (a) wood density, (b) total bark density, and (c) total bark thickness. The concentration of starch against (d) wood density, (e) total bark density, and (f) total bark thickness. The concentration of NSC (the sum of that of soluble sugars and starch) against (g) wood density, (h) total bark density, and

(i) total bark thickness. Black and white circles indicate values for branch and trunk, respectively. Error bars represent 1 standard error (SE). The solid and dotted curves indicate significant and marginally-significant relationships among traits, respectively. The lines in (a), (d), (e), (g), and (h) were fitted by the standardized major axis regression. The solid and dashed trends in (a) and (g) indicate the trends excluding the species with the lowest wood density (*Canarium subulatum*), denoted by black arrows. Note that scale is different for starch (g concentration). †  $0.05 \leq P < 0.10$ , \*  $P < 0.05$

2002; Hartmann and Trumbore 2016). For example, species-specific sink activities such as preparation for leafing or flowering (an internal factor) will drive the branch NSC and thus hide the relationships between PLC and NSC in branches.

### Coordination between sapwood density, bark morphology, and NSC reserves

Consistent with the positive linkages between hydraulics and NSC levels (Fig. 2) and with WD – PLC relationship

(Fig. 1), the concentrations of soluble sugars and NSC within trunk xylem decreased linearly with WD (Fig. 3). These results suggest that sapwood density underlies species differences in NSC reserves, possibly through its influence on xylem water transport. The starch concentrations in the branch xylem were weakly and positively correlated with WD (Fig. 3d) and were not significantly correlated with xylem hydraulics among species (Fig. 2c, d). Therefore, branch hydraulics would not explain the observed variation in starch concentrations. These facts may indicate that most of the starch is stored within living fibers, possibly



contributing to embolism resistance and avoidance from carbon depletion (Pratt and Jacobsen 2017).

We expect that species with denser and thicker bark maintain phloem transport capacity and relatively high NSC concentrations in both branch and trunk xylem during the dry season among woody plants, because such hard bark might provide high mechanical resistance to phloem deformation (Hacke et al. 2001). There was a positive relationship between NSC concentrations and BD in the branch (Fig. 3h). However, this relationship was not observed in the trunk. Rather, the dense-barked species showed low starch levels in the trunk (Fig. 3e). This suggests that, in contrast to our expectation, dense-barked species greatly lose phloem transport capacity greatly during drought, resulting in the accumulation and reduction of NSC in branches and trunks, respectively. Given the positive correlation between sapwood and bark density (Table 2), it is further suggested that species with dense wood and bark in branch show low drought resistance in the transport capacity of both water (Fig. 1a) and photosynthates.

## Ecological implications

The variability of rainfall seasonality, including the magnitude, timing of onset, and duration of the dry season, has recently increased in SDTFs (Feng et al. 2013). Intensified drought induces changes in forest composition based on species desiccation resistance (Phillips et al. 2010; McDowell et al. 2018). Our study reveal that sapwood density is a useful proxy for the safety of xylem water conduction and NSC reserves in SDTF trees. If the drought period and intensity during the dry season continue to increase, tree species with high WD would face a greater risk of drought-induced mortality in terms of water conduction and stored NSC (Figs. 1 and 2). Thus, under ongoing global warming, the recent increase in prolonged drought events may select for tree species with low to medium WD. Recent some studies have demonstrated increasing abundance of deciduous tree species, which have typically low WD (Méndez-Alonzo et al. 2012) in SDTFs (Fauset et al. 2012; Aguirre-Gutierrez et al. 2019), leading to the changes of forest structure and functions.

## Conclusion

Among the examined 13 deciduous tree species in SDTF, (1) xylem hydraulic properties are coordinated with NSC reserves during the dry season and (2) sapwood density underlies these functional divergences. Sapwood density (WD) is a robust and useful proxy for the species sensitivity to drought stress among tree species in SDTFs. Woody plants with high WD have been often recognized as

dehydration-tolerant trees globally (e.g., Greenwood et al. 2017; O'Brien et al. 2017). However, our study showed that heavy-wooded species would be sensitive to drought stress. Future studies are needed to clarify when and where tree species are highly tolerant/vulnerable to extreme drought under recent rapid global warming, in relation to WD.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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