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Centralblatt
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Forstwesen**Stem respiration and chemical composition in *Dalbergia Odorifera*
plantations differing in soil moisture content**ZY Cui ^{1,2*}, ZJ Yang ¹, DP Xu¹, RC Xi ², NN Zhang ¹, XJ Liu ¹ & Z Hong ¹**Keywords:** *drought, nitrogen, non-structural carbohydrates,
stem respiration***Abstract**

Few study examined the possible influence of artificially altering soil moisture content on stem respiration (R_s) and stem chemical composition together, we artificially simulated four soil moisture gradients in *Dalbergia odorifera* (*D. odorifera*) plantations and investigated R_s , predawn shoot water potential (ψ_{pd}), nitrogen content, and non-structural carbohydrates (NSCs) over time. Stem temperature (T_s) and R_s declined continuously during the dry period and reached their minimum values in January. Irrigation increased the R_s rate, while drought decreased it. The nitrogen content of the sapwood remained constant until December, after which it decreased when winter began. During the winter, the sapwood nitrogen increased under irrigation but

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decreased under drought conditions. The soluble sugars tended to increase during the dry period at the cost of starch, which caused a small but non-significant increase in NSCs. The effect of water treatments on total NSCs was limited; however the drought treatments increased the soluble sugars content but decreased the starch content. R_s explained 49, 72 and 40% of the seasonal variation in the stem nitrogen, starch and soluble sugars, respectively. The ψ_{pd} significantly explained 49, 79 and 85% of the variation in the R_s , stem starch and soluble sugars, respectively. Thus, soil moisture content likely affects R_s by affecting the amount of sapwood nitrogen, starch and soluble sugars. Low soil moisture content induced by drought enhanced the transformation of starch to soluble sugars during the winter, when heartwood formed. These strong relationships may provide interesting implication for future study on heartwood formation.

1. Introduction

Dalbergia odorifera T. Chen (*D. odorifera*) is a medium-sized evergreen tree of the Leguminosae family, which is famous for its heartwood. The heartwood of *D. odorifera*, named "Jiang Xiang" in traditional Chinese medicine, has been included in the Chinese Pharmacopoeia for centuries. The heartwood of *D. odorifera* is widely used to stop bleeding, regulate the "Qi", dissipate blood stasis, and relieve pain (Tao & Wang 2010). *D. odorifera* has been widely used not only as a kind of medicinal material in the pharmaceutical industry but also as a preferred material in luxury furniture and crafts. However, the heartwood of *D. odorifera* forms relatively slowly; thus, research has focused on the promotion of heartwood formation (Cui et al. 2016).

Stem respiration (R_s) is an important component of tree physiology, accounting for 5 ~ 40% of total annual respiration among different forests (Maseyk et al. 2008, Wieser et al. 2009, Guidolotti et al. 2013). Some field studies have suggested that R_s declines with decreasing soil water content (Levy and Jarvis 1998, Stahl et al. 2011), but not others (Zach et al. 2010, Guidolotti et al. 2013). Discrepancies may arise from the distinct sensitivity of species to water deficit and the lack of studies examining the relationship between tree water availability and R_s . In addition, studies on the effects of irrigation on R_s in the dry season are limited (Maier 2001).

R_s is often correlated with sapwood nitrogen content (Ryan 1991, Vose and Ryan 2002) probably because protein turnover and other processes related to protein metabolism. However, a relationship between R_s and nitrogen content is not always observed in field grown trees. Lavigne and Ryan (1997) found no relationship between R_s and sapwood nitrogen content in several boreal tree species. In contrast, winter stem R_s was correlated with sapwood nitrogen content in eastern white pine (*Pinus strobus* L.) trees (Vose and Ryan 2001). Experimental data examining effects of soil moisture content on sapwood nitrogen content is limited. Sapwood nitrogen

content decreased significantly following drought (Rodríguez-Calcerrada et al. 2014), and it was also observed in stems of beech (*Fagus sylvatica* L.) seedling (Peuke and Rennenberg 2004).

Non-structural carbohydrates (NSCs) can account for up to 20% stem tissue biomass (Kozłowski 1992). NSCs in stem tissue are intrinsically linked to many physiological processes in plants, and may fluctuate considerably in response to variations in respiration (Pregitzer et al. 2000), however little is known on the relationship between R_s and NSCs in stem tissue (Rodríguez-Calcerrada et al. 2014). Although there are a few cases where tree NSCs show a decline in response to drought (Körner 2003, Anderegg 2012), observations of increased NSCs during drought are much more common in the literature (Würth et al. 2005, Sala and Hoch 2009, Galvez et al. 2011). Experimental studies on seedlings have indicated that an increase in nonstructural carbohydrates (NSCs) in plant bodies enhances their drought tolerance (Secchi and Zwieniecki 2011, O'Brien et al. 2014). However, the contribution of NSCs to drought tolerance in mature trees remains controversial, because studies monitoring variations in NSCs and xylem embolism over time are lacking.

To our knowledge, few study examined the possible influence of artificially altering soil moisture content on all of these variables together. In this study, we measured dynamic changes in R_s , water potential, nitrogen content, and NSCs in contrasting soil moisture conditions continuously during the dry season from 2016 to 2017. The objectives of this study were to (1) investigate the variation patterns of R_s , water potential, nitrogen content, and NSCs (2) present new data on the effects of altered soil moisture content on R_s , water potential, nitrogen content, and NSCs in stem tissue during the dry period; (3) determine the possible relationships among R_s , water potential, nitrogen content, and NSCs.

2. Materials and methods

2.1 Plant material and study area

The study site was a young 8-year-old plantation of *D. odorifera*, when the heartwood formation begins. The plantation was located in Foshan, Guangdong Province, in southern China (22°47'N, 112°32'E). The mean annual precipitation is 1681.2 mm, with 562 mm occurring in the dry season (from October to March). The mean annual air temperature is 23.4°C, with the minimum in January (19.3°C) and the maximum in July (33.8°C). In 2009, 1-year-old seedlings of *D. odorifera* were bought from Hainan Island (the origin) and the plantation was established using an approximately 2.5-m × 2.5-m planting grid. The plantation presented a survival rate of 95% and had a 7.68 ± 0.43 cm mean stem diameter at breast height (DBH) at the beginning of treatments and 4.21 ± 0.36 m mean tree height. For R_s measurement, two trees were selected in

the central region of each plot, i.e., six sampled trees of each regime were chosen in the middle of three plots. The mean DBH at the beginning of treatments was 8.8 ± 0.7 cm for HD trees, 8.5 ± 0.4 cm for LD trees, 9.0 ± 0.8 cm for DI trees, and 8.4 ± 0.5 cm for CK trees. The slope of plots was approximately 15° , and ground vegetation was dominated by *Polygonum chinense* and *Bidens pilosa*. The soil is a latosol (developed from granite) with a depth > 1 m. Characteristics of the site are listed in Table 1.

Table 1: Climate, forest conditions and soil physical and chemical properties of the study region

Site	Longitude	Latitude	Temperature	Rainfall	Sunshine	Frost-free
	112°32' E	22°47' N	23.4°C	1681.2 mm	1,914 h yr ⁻¹	360 d yr ⁻¹
Stand	Age	Area	Density	Survival	DBH	Height
	8 years old	100 hm ²	2.5 m * 2.5 m	95%	7.68 ± 0.43 cm	4.21 ± 0.36 m
Soil (0~30cm)	SBD	OM	PH	Available N	Available P	Available K
	1.3 ± 0.1 g·cm ⁻³	6.2 ± 0.3 mg·kg ⁻¹	4.5 ± 0.1	25.7 ± 0.8 mg·kg ⁻¹	8.7 ± 0.2 mg·kg ⁻¹	64.3 ± 1.1 mg·kg ⁻¹

SBD = soil bulk density, OM = organic matter; DBH, height and soil physical and chemical properties are each presented as mean ± standard error

2.2 Experimental design and soil moisture content

The experiment was a completely randomized block design. To widen the range of the soil moisture status during the dry season, we arranged four regimes with three blocks, resulting in a total of 12 plots of 400 m² each: (1) heavy drought (HD), in which $\approx 74.8\%$ of rainfall was intercepted by 2-m-diameter polyvinyl chloride (PVC) rain gutters that conducted water away from three plots; (2) light drought (LD), in which $\approx 46.1\%$ of rainfall was intercepted by 1.3-m-diameter PVC rain gutters that conducted water away from three plots; (3) dry season irrigation (DI), in which an amount of water equal to the monthly rainfall water was intercepted by the HD setup and diverted to three plots for irrigation from October 2016 on; (4) and the control (CK). The four treatment plots of the same block were 5 meters apart from each other. The throughfall exclusion system has been described previously (Limousin et al. 2009, Rodríguez-Calcerrada et al. 2011). In each plot, there is about 60 trees, and eight rain gutters of 20 meters long were installed one meter high from the ground. To avoid the lateral water movement into the dried out plot as possible, all plots were chosen

on the upper slopes and each plot was separated by water-stop sheets of 3 meters long and 2 meters wide. Soil volumetric moisture content was monitored by a soil moisture monitoring system (AZS-2C, TDR, China) at a depth of ≈ 30 cm once per hour. In each plot, three sensors were installed in 3 different positions. Each sensor was installed 1 m far from the tree base in the same direction under the gutters.

2.3 Stem respiration

The R_s at 1.3 m was measured in situ using an LI-8100 CO₂ flux system (Li-Cor Inc., Lincoln, NE, USA) in 2-week intervals as described previously by Xu et al. (2000). A custom-built cylindrical polyvinyl chloride (PVC) collar of 8 cm in diameter and 10 cm in height was attached to the stem surface to connect the stem and the LI-8100 CO₂ flux system. The two ends of the opaque PVC collar were cut to match the approximate curvature of the stem and the LI-8100 CO₂ flux system. The collar was attached to the stem using silicone sealant, and was maintained in the same location throughout the study period. The measurements (randomization between treatments, block by block) occurred from 9:00 to 12:00 from October 2016 to March 2017 (The sunrise is between 6:40 and 7:10). T_s at a depth of 1 cm was also measured simultaneously at each sampling location using a portable electronic thermometer, the thermometer has a sharp probe, which can make sure good contact with the wood. The R_s and T_s were uniformly measured on south-facing stems in this study.

The Q_{10} values were used as a parameter of temperature sensitivity of the stem with the following the equation:

$$Q_{10} = \exp(10k)$$

with "k" being the slope of the regression equation of R_s against T_s (Atkin et al. 2005).

2.4 Water potential

On the same days of every R_s measurement in 2-week intervals, one shoot from each tree in which the R_s was measured was excised before dawn and immediately measured using a pressure chamber (PMS Instrument Company, Albany, OR, USA).

2.5 Chemical composition

To avoid affecting the measurement of R_s , stem cores (the outer 1 cm of sapwood) at breast height of 4 ~ 5 surrounding trees belonging to each treatment were collected by a stem corer every two weeks. Samples were collected between 9:00 and 12:00 to

minimize the diel variation in NSCs, we immediately chilled them on ice, and then microwaved them for 90 s at 600 W within 2 h of collection to stop carbohydrate enzymatic reactions (Hoch et al. 2003), after which the samples were oven-dried at 65 °C to a constant weight. We ground the dried tissues to a fine powder and stored at 4 °C until analyses. The nitrogen content was measured using an elemental analyzer (Flash EA1112, USA). The NSCs (soluble sugars and starch) were analyzed using the enzymatic assay of McCleary et al. (1997) as described previously by Yang et al. (2015).

2.6 Statistical analysis

The mean values and standard errors were calculated and analyzed. The equations for the calculations and the plots for the graphs were generated in Microsoft Excel 2010 (USA); the analysis of variance and regression analysis were performed using the data processing software SPSS 17.0 (IBM, NY, USA).

3. Results

3.1 Soil moisture content and shoot water potential

An overall decreasing trend in soil moisture content was observed during the dry period, with the minimum values occurring in February (Figure 1a). The soil moisture content was significantly lower for the HD and LD treatments subjected to through-fall exclusion but higher for DI ($P < 0.01$). This decrease in soil moisture content caused continuous decline in the shoot water potential (ψ_{pd}) during the dry period. Significant differences in soil moisture content caused significant differences ($P < 0.01$) in the shoot water potential (ψ_{pd}) among water treatments from the end of November to February (Figure 1b).

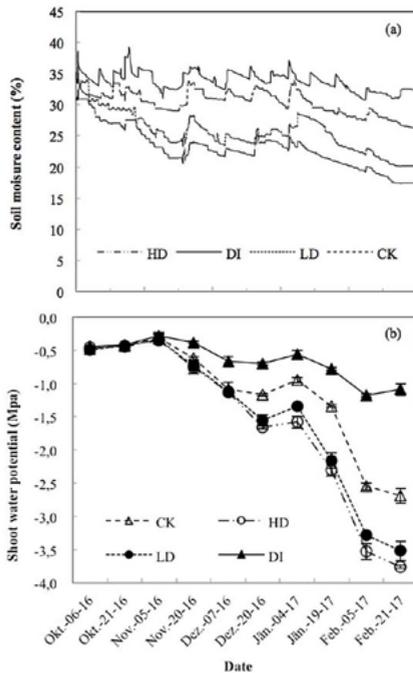


Figure 1: Soil moisture content (a) and predawn shoot water potential (ψ_{pd}) (b) during the dry period (2016-2017). Values of ψ_{pd} are the means \pm SE ($n = 6$).

3.2 Stem temperature and respiration

The results showed that the values of Q_{10} varied over the dry season without a clear pattern (Figure 2). T_s decreased continuously during the dry period and reached its minimum value in January (Figure 3a). We found no significant differences in T_s among water treatments except in December and January ($P < 0.05$), which are in the coldest period of the year (Figure 3a). The seasonal variation patterns of R_s were similar to those of T_s (Figure 3b). From the end of October, R_s significantly differed among water treatments (Figure 3b). We found that the R_s differed significantly ($P < 0.05$) among water treatments, following the order $DI > CK > LD > HD$ (Figures 3b).

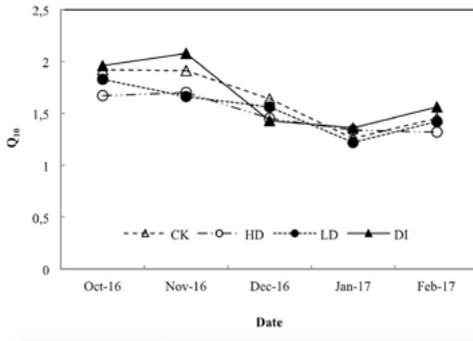


Figure 2: Seasonal variation of sensitivity of stem respiration (R_s) to variations in temperature (Q_{10}).

3.3 Chemical composition

The sapwood nitrogen content remained constant until December, after which it decreased as winter began. Significant differences ($P < 0.05$) were found in sapwood nitrogen content among water treatments in December and January (Figure 3c). A decreasing trend for sapwood starch (Figure 4a) and an increasing trend for soluble sugars (Figure 4b) were observed through the sampling dates, which caused a small but non-significant increase ($P > 0.05$) in the total NSCs (Figure 4c). Significant variations in starch and soluble sugars were observed among water treatments; however, there were no significant differences between DI and CK or HD and LD (Figure 4a, 4b). No significant difference was observed in the total NSCs among treatments (Figure 4c).

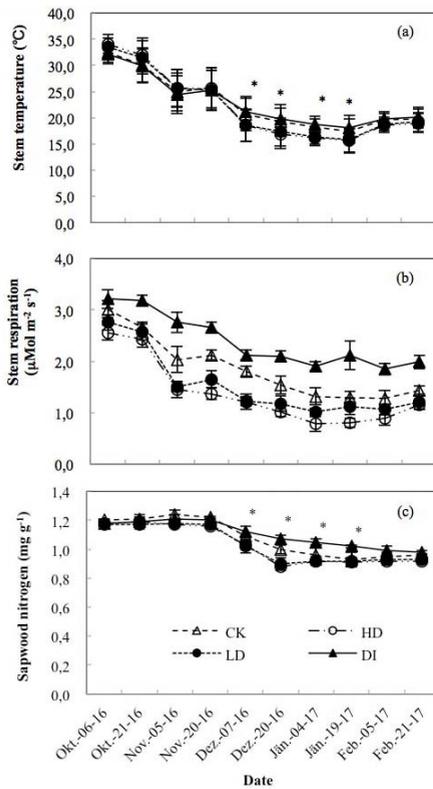


Figure 3: Stem temperature (T_s) (a), respiration (R_s) (b) and nitrogen content (c) during the dry period. Values are the means \pm SE ($n = 3-6$). "*" indicates significant differences ($P < 0.05$) among the CK, HD, LD and DI treatments

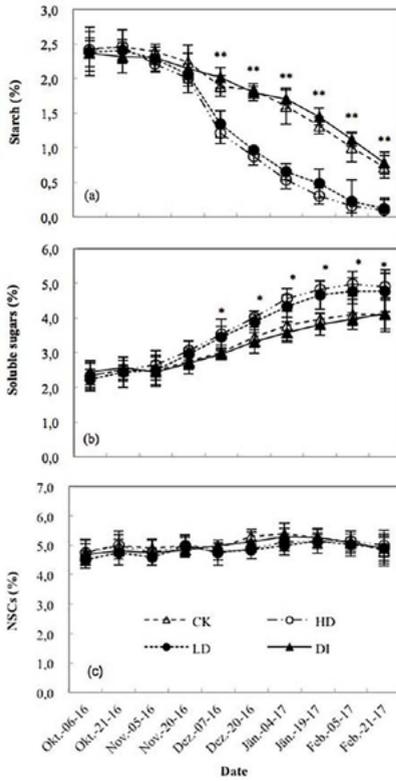


Figure 4: The concentrations of starch (a), soluble sugars (b) and non-structural carbohydrates (NSCs) (c) in the sapwood during the dry period. Values are the means \pm SE ($n = 3$). “%” means % dry mass of sapwood. “*” and “**” indicate significant differences at the 0.05 and 0.01 levels, respectively, among the CK, HD, LD and DI treatments.

3.4 Relationship among water potential, respiration and chemical composition

The seasonal pattern of R_s was related to the seasonal changes in stem nitrogen, starch and soluble sugars. R_s explained 49, 72 and 40% of the seasonal variation in the stem nitrogen, starch and soluble sugars, respectively (Figure 5). The variation in ψ_{pd} significantly ($P < 0.05$) explained 49, 79 and 85% of the variation in R_s , starch and soluble sugars during the dry period, respectively (Figure 6).

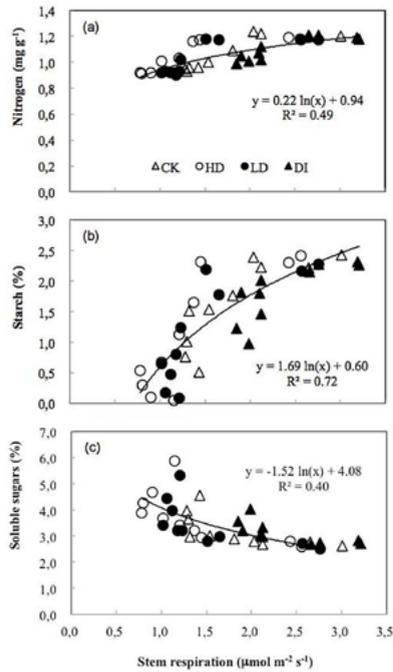


Figure 5: Relationships between stem respiration (R_s) and the concentrations of nitrogen (a), starch (b) and soluble sugars (c) in the sapwood. “%” means % dry mass of sapwood. $P < 0.05$ for all regression equations.

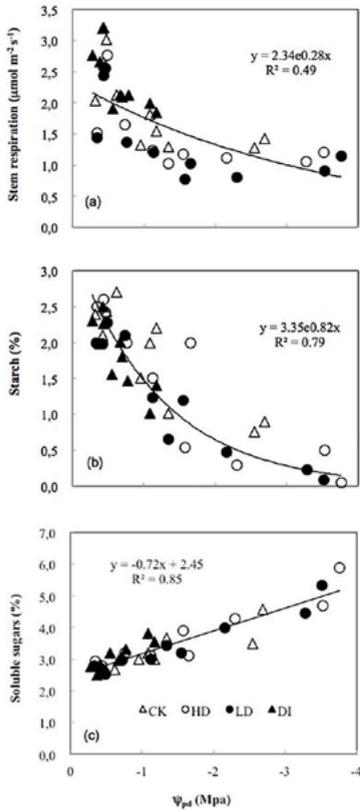


Figure 6: Relationships among predawn shoot water potential (Ψ_{pd}) and stem respiration (a), starch (b) and soluble sugars (c). “%” means % dry mass of sapwood. $P < 0.05$ for all regression equations.

4. Discussion

4.1 Seasonal changes in stem respiration and chemical composition

The similar seasonal pattern of moisture condition of soil and trees indicate that soil moisture content had a significant and positive effect on the moisture condition of trees (Granda et al. 2014, Rodríguez-Calcerrada et al. 2014). During the dry season, the decreasing temperature decreased stem respiration by inhibiting the enzyme activity (Gaumont-Guay et al. 2006). The sapwood nitrogen content decreased as winter began. Maier (2001) also observed sapwood nitrogen to decrease with T_s during the winter. This decrease in sapwood nitrogen was likely caused by a progressive reduction in the demand for energy from physiological processes. A decreasing trend

for sapwood starch and an increasing trend for soluble sugars were consistent with the data of Terziev et al. (1997), which caused a small but non-significant increase ($P > 0.05$) in the total NSCs (Hoch et al. 2003). Soluble sugars in the sapwood tended to increase during the dry period at the cost of starch (Sevanto et al. 2014).

4.2 Changes in stem respiration and chemical composition in response to altered soil moisture content

Hartmann et al. (2013a) observed that drought could reduce whole-plant respiration. Drought can also slow R_s rates by reducing xylem CO_2 concentrations (Teskey and McGuire 2005; Saveyn et al. 2007a), respiratory substrate availability (Wertin and Teskey 2008; Maier 2001), phloem transport (Sevanto et al. 2014), and energy demands of cell maintenance processes (Atkin & Macherel 2009). Drought-induced low turgor pressure of living cells (Zweifel et al. 2006) could also be a factor underpinning low R_s (Saveyn et al. 2007a, 2007b). However, studies on the effects of irrigation on R_s are limited. Maier et al. (1998) observed that R_s increased in response to irrigation and fertilization treatments during the dormant season; however, irrigation did not have a significant effect on R_s during the growth season (Maier 2001). These results were consistent with our observation that DI increased the R_s rate during the dry period. During the same period, low soil moisture content was the main factor limiting the physiology of the trees, but this factor was eliminated in the DI treatment. In addition, a number of mechanisms maintaining stem functionality might regulate respiratory metabolism (Rodríguez-Calcerrada 2014). Thus, the irrigation-induced increase in R_s was likely caused by a progressive increase in the energy demand from physiological processes.

Interestingly, we found no significant differences in either T_s or sapwood nitrogen content among water treatments except in December and January ($P < 0.05$), which are in the coldest period of the year (Figure 3a, 3c). HD and LD trees with lower water potential were more vulnerable to sudden drops in temperature in December and January, and this vulnerability resulted in significantly lower T_s values for trees in the HD and LD treatments compared with those for trees in the CK and DI treatments. A positive correlation exists between T_s and sapwood nitrogen in winter (Maier 2001). Ultimately, significant differences in T_s caused by sudden temperature drops resulted in significant differences in sapwood nitrogen during the winter.

In this study, the effects of water treatments on the total NSCs were very limited; however drought treatments increased soluble sugars but decreased the starch content. Observations of NSC concentration changes in trees during drought are rather inconclusive, though; concentrations may increase or decrease or not change at all (Galvez et al. 2011, Poyatos et al. 2013, Mitchell et al. 2013, Rodríguez-Calcerrada et al. 2014) and this response can even vary across plant organs of individual trees (Hartmann et al. 2013b). The phenomenon that drought increased soluble sugars but decreased the starch content has also been observed by Sala and Hoch (2009) and

Rodríguez-Calcerrada et al. (2014).

4.3 Relationship between stem respiration and chemical composition

The decrease in stem nitrogen coincided with reductions in R_s during the dry period. The relationship between R_s and stem nitrogen varies for other species. R_s is not related to stem nitrogen in *Picea abies* (Stockfors & Linder 1998) or in several other boreal species (Lavigne & Ryan 1997). However, Ryan (1991) showed that respiration in several plant tissues increased linearly with tissue nitrogen. R_s also increased with stem nitrogen in *Pinus strobus* (Vose & Ryan 2002) and loblolly pine (Maier 2001). If the stem nitrogen is indicative of protein content (Penning de Vries 1975) and protein metabolism consumes the largest portion of R_s in woody tissues (Maier 2001), then changes in nitrogen might result in significant changes in R_s . In our study, R_s varied with stem nutrition. This variance may cause serious errors when estimating the R_s of *D. odorifera* stands growing under different nutrient regimes; thus, other methods of estimating stand R_s may be needed.

NSCs are intrinsically linked to many physiological processes in plants and can fluctuate considerably in response to variations in R_s (Pregitzer et al. 2000). R_s is significantly related to the soluble sugar content in the leaves and roots of many tree species (Atkin and Tjoelker 2003, Kruse et al. 2011) but has rarely been examined in stems (Gansert et al. 2002). To our knowledge, few studies have compared the effects of drought or irrigation on R_s together with NSCs (see Rodríguez-Calcerrada et al. 2014). Rodríguez-Calcerrada et al. (2014) did not find a significant relationship between R_s and NSCs. In our study, R_s explained 72 and 40% of the variation in the starch content and soluble sugar content during the dry period, respectively. This discrepancy might be attributed to differences in the study period and tree species. Future studies comparing the effects of drought or irrigation on R_s together with NSCs are warranted. Based on the strong relationships among R_s , sapwood nitrogen, starch and soluble sugars, soil moisture content likely affects R_s by affecting the sapwood nitrogen, starch and soluble sugars.

4.4 Interesting implication for future study

As is well-known, heartwood formation is a secondary metabolic process. "Jiang Xi-ang", the heartwood of *D. odorifera*, contains volatile oils and flavonoids. These secondary metabolites are likely reflected by NSC accumulation because of decreased growth and sink activity (Herms & Mattson 1992). In other words, NSCs bridge the conversion of photosynthetic products to secondary metabolites through the transformation of starch to soluble sugars (Hartmann & Trumbore 2016). Abundant evidence has suggested that heartwood forms during the dormant or dry season (Shain & Hillis 1973, Nelson 1978, Beauchamp et al. 2013), when stems require more secondary metabolic substrates obtained by the transformation of starch to soluble sugars. Meng et al. (2010) investigated *D. odorifera* in multiple locations and obser-

ved that drought could promote heartwood formation in *D. odorifera*. In our study, low soil moisture content induced by drought enhanced the transformation of starch to soluble sugars during winter. These strong relationships could provide data to support the hypothesis that drought promotes heartwood formation in *D. odorifera*. Further studies on the effects of drought on altered NSC levels in different zones of the stems and the possible relationships of these phenomena with heartwood formation are warranted. In addition, based on the significant relationship between R_s and NSCs (starch and soluble sugars), variation in the R_s rate may also indicate changes in heartwood formation during the dry period.

5. Conclusions

In addition to total NSCs, significant seasonal variation could be observed in R_s , water potential, nitrogen content, starch and soluble sugars. Irrigation increased while drought decreased R_s . Drought only affected nitrogen content during the winter. The effect of soil moisture content on total NSCs was limited; however drought enhanced the transformation of starch to soluble sugars during the dry period. These strong relationships among R_s , water potential, nitrogen content, starch and soluble sugars may provide interesting implication for future study on heartwood formation. Further studies on the effects of drought on the radial distribution of NSC levels in the stems and the possible relationships of these phenomena with heartwood formation are warranted.

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