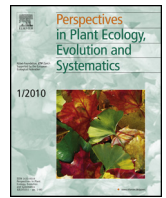




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## Research article

# Physiological homeostasis and morphological plasticity of two tree species subjected to precipitation seasonal distribution changes



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## ABSTRACT

General circulation models and empirical observations show that rainfall patterns will become increasingly erratic in the future as the paradigm “dry gets drier, wet gets wetter” becomes globally prevalent. Currently, few field studies have evaluated the long-term effects of extreme precipitation on forest ecosystems based on tree physiology. To provide a better mechanistic understanding of these effects, a two-year “Precipitation Seasonal Distribution Changes” experiment (PSDC) was conducted in lower subtropical China. The treatments included “Drier dry season and wetter wet season (DD)”, “Extended dry season and wetter wet season (ED)” and “Ambient control (AC)”. The throughfall of the DD treatment was excluded during the dry season (October–March of the following year) to simulate drought, whereas the throughfall of the ED treatment was excluded in the spring (April–May) to simulate spring drought without significant altering the total annual precipitation input. The sap flow, water use efficiency, leaf and wood nutrient content and morphological parameters of two co-occurring tree species, *Michelia macclurei* Dandy and *Schima superba* Gardner & Champ., were quantified to elucidate the physiological mechanisms that occur in response to rainfall pattern changes. Our results indicated that the whole-tree transpiration per unit sapwood area ( $J_s$ ) and intrinsic water use efficiency ( $WUE_i$ ) showed homeostatic responses. Tree transpiration and response parameters to environmental variables (vapor pressure deficit [VPD] and photosynthetically active radiation [PAR]) did not show significant treatment effects regardless of drought, spring drought or irrigation periods. However, the leaf nitrogen ( $N_{area}$ ) and phosphorus ( $P_{area}$ ) content showed fluctuations, particularly the leaf N:P ratio, which showed that rainfall pattern changes had adverse effects on nutrient acquisition in this dual nitrogen- and phosphorus-limited forest ecosystem. The wood stoichiometry was more conserved than the leaf stoichiometry. For a given leaf  $^{13}C$  discrimination ( $\approx c_l/c_a$ ), the wood  $^{13}C$  discrimination did not show treatment or species effects, suggesting that the carbon transfer of trees was not affected by rainfall patterns. The branch  $A_s:A_l$  was significantly negatively correlated with the parameters representing the sensitivity of tree transpiration to VPD, indicating that the trees maintained homeostatic responses by combining stomatal control and morphological adjustments. In mesic environments, the two studied tree species showed high resilience to seasonal rainfall pattern changes and homeostatic responses to nutrient acquisition, light use and water uptake, which is consistent with the ‘ecohydrological equilibrium theory’. In conclusion, the shallow-rooted *M. macclurei* presented a growth advantage in mesic environments or under mild water stress, whereas the deeply rooted *S. superba* is more competitive under predicted prolonged drought scenarios, such as DD and ED rain patterns, because of its greater morphological plasticity and increased water uptake from groundwater. Both species are common in south and eastern China but present inherently different responses to seasonal precipitation changes, which implies that changes in the timing and magnitude of precipitation may have consequences for plant nutrient acquisition and water balance and the potential to alter community composition.

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## 1. Introduction

Greenhouse gas emissions caused by human activity and global warming will exacerbate the unequal distribution of global rainfall (Marvel and Bonfils, 2013; Zhang et al., 2013), which will lead to intensified droughts in subtropical and tropical regions in the northern hemisphere (Zhang et al., 2007). General circulation models (GCMs) and field observations have shown that rainfall patterns are changing in frequency and intensity with increasing significance (Huntington, 2006). Extreme rainfall events can have a significant effect on the structure and function of forest ecosystems, particularly for subtropical regions of southern Asia, which is an area sensitive to climate change (Piao et al., 2010; Zhou et al., 2011). However, empirical studies rarely evaluate the possible effects of these rainfall events (Beier et al., 2012). In southern China, the future rainfall pattern will show a “dry gets drier, wet gets wetter” paradigm (IPCC, 2007; Zhou et al., 2011). For example, recent studies have shown significantly lower rainfall levels during the dry season in the Pearl River Delta region of southern China and increased extreme rainfall, whereas the annual rainfall level remains basically unchanged, showing an overall trend of increasing drought (Gemmer et al., 2011).

Extreme rainfall can change hydrological processes, such as runoff, soil evaporation and infiltration, which results in altered tree physiology, plant composition and interactions and community structure (Smith et al., 2009). For example, in the southwestern United States, large-scale tree mortality was caused by droughts in 1996 and 2002, and the mortality of piñon was 6.5-times higher than that of juniper, which resulted in juniper-dominated vegetation (Mueller et al., 2005). A 3-year rainfall manipulation experiment showed that both piñon and juniper had similar responses to available soil water during photosynthetic acclimation; however, reduced rainfall was more detrimental to piñon growth because of its low physiological resilience (Limousin et al., 2013). The effects of extreme rainfall on different forest ecosystems are also linked to the nature of the ecosystem itself. Model predictions show that extreme rainfall reduces soil moisture in moist ecosystems, which is mainly because of increased rainfall event intervals and runoff. However, extreme rainfall increases soil moisture in arid ecosystems, which is mainly because of increased infiltration and reduced evaporation (Knapp et al., 2008). These contrasting hydrological effects can have different effects on plant physiology and plant community dynamics; however, changing soil moisture will not necessarily produce a corresponding physiological response. For example, in a water affluent ecosystem, *Castanopsis acuminatissima* did not decrease stomatal conductance ( $g_s$ ) in response to decreased soil moisture, which was mainly because of the dampening effect of drought in a humid environment (Schuldt et al., 2011). In a cacao/*Gliricidia* stand in Indonesia, the water use, leaf litterfall and soil CO<sub>2</sub> flux did not change under a throughfall reduction, suggesting that a moist forest ecosystem has a certain resistance to rainfall pattern changes (Schwendenmann et al., 2010).

Changes in rainfall patterns can also have an important influence on ecological processes, such as soil respiration, net nitrogen and phosphorus mineralization, net primary productivity and net ecosystem exchange (Knapp et al., 2008). Rainfall pattern changes can affect the relationship above- and belowground and thus the biogeochemical cycles, i.e., carbon and nutrient cycling, which may become decoupled (cf. review by Nielsen and Ball, 2015). Persistent drought caused by extreme rainfall can change the water holding capacity and microbial communities of the soil (Sowerby et al., 2008). Available soil water can dramatically change the soil's net nitrogen mineralization, particularly in the transition between wet and dry seasons (Marrs et al., 1991). Under lower moisture conditions, soil acid phosphatase can decrease by 31–40% and protease

activity of 35–45% and urease activity of 42–60% can decrease by 21%, indicating that a small change in soil moisture can significantly affect enzyme activity and thus affect plant nutrient uptake or indirectly affect plant growth (Sardans and Peñuelas, 2005). In a study on the leaf nutrient content of European beech (*Fagus sylvatica* L.), Meier and Leuschner (2014) observed that the soil's organic nitrogen and phosphorus pool decreased with rainfall decreases, whereas the leaf nitrogen and phosphorus content did not fluctuate with soil moisture. The lower leaf N:P ratio was attributed to soil phosphorus pool variations. Extreme rainfall can increase soil leaching, thus reducing the supply of soil nutrients. Prolonged drought can also reduce nitrogen and phosphorus absorbance as well as many metabolic nutrient processes, thus changing the characteristics of leaf stoichiometry (Sardans and Peñuelas, 2012). Plants that have phosphorus and potassium nutrient content stability have a competitive advantage over those without stable nutrient contents (Ghandilyan et al., 2009). Because of plant adaptations and resilience, nutrient acquisition will remain stable; therefore, the occasional reduced rainfall will affect stoichiometry more than ontogeny or phenology (Sardans et al., 2013). Therefore, rainfall pattern changes can indirectly affect soil nitrogen and phosphate content or directly alter plant nutrient uptake. However, there is little empirical research on the stoichiometry of tree components under rainfall manipulation scenarios.

Trees typically respond to extreme water stress through stomatal regulation, aboveground morphological adjustments and root-based processes. A rapid and transient response is stomatal closure to avoid water loss (Sperry, 2004). Stomata are sensitive to environmental factors, and sensitivity to the vapor pressure deficit (VPD) affects plant growth (Franks and Farquhar, 1999). Tree transpiration relative to VPD can help plants maintain the minimum leaf water potential and hydraulic conductivity and thus resist drought-induced embolism (Addington et al., 2004; Gao et al., 2015; Oren et al., 1999). Plants that have strong stomatal control can adapt well to mesic environments because they can increase transpiration under low VPD or increase their growth rate. A medium drought response and adaptive strategy includes leaf shedding (Limousin et al., 2009, 2010), which is equivalent to enhancing the whole-tree or branch sapwood area to leaf area ratio ( $A_s:A_l$ ) (Martínez-Vilalta et al., 2009). Higher  $A_s:A_l$  could partially compensate for the negative effect of increased flow-path length with tree size, thus ensuring a stable hydraulic continuum (Ewers et al., 2005; McDowell et al., 2002; Schäfer et al., 2000). For example, Martin-StPaul et al. (2013) observed the Mediterranean oak (*Quercus ilex*) in natural plots, and the plots that excluded throughfall showed consistent physiological responses. However, in the drought treatment plots, the branch  $A_s:A_l$  increased significantly. Cork oak (*Quercus suber*) transpiration decreased by 10% or increased from 11 to 20% with rainfall manipulation (– or +); however, differences in the leaf water potential or gas exchange parameters were not observed in the different rainfall treatments, indicating that oak trees have a greater resistance and resilience to rainfall pattern changes (Besson et al., 2014). A long-term adaptive strategy is to alter the root distribution (Martin-StPaul et al., 2013). Padilla et al. (2015) observed that rainfall reduction could increase the root length density and production. In addition to changing root distribution and growth, plants tend to uptake deeper water in water-stressed scenarios (Barbeta et al., 2015; Hasselquist et al., 2010; Romero-Saltos et al., 2005). However, rainfall patterns or soil moisture changes do not indicate the corresponding changes in the tree's water use strategies or physiological parameters (Anderegg et al., 2013; Fisher et al., 2007; Schwendenmann et al., 2010). Thus, trees have been reported to maintain a xylem hydraulic continuum or homeostatic responses to water stress through stomatal control or morphological adjustments (Carter and White, 2009; Limousin et al., 2012).

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