



Full Length Article

Resource Trade-off in *Cotinus coggygia* Seedlings under Drought Conditions—**Phenotypic** Plasticity of Leaf and Fine Root Functional Traits

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Abstract

A field experiment was performed in which five different *Cotinus coggygia* seedling populations were subjected to both drought and well-irrigated treatments. The phenotypic plasticity of leaf and fine root functional traits related with morphology, biomass allocation and seedling overall performance (*i.e.*, seedling total dry biomass) were evaluated. The results showed the plasticity of specific fine root length, root length ratio, root length/leaf area, root biomass fraction, root biomass/leaf biomass and leaf biomass fraction were the key determinants driving the plasticity of seedling overall performance. The correlation between the plasticity of leaf area ratio and fine root length ratio was an indicator of the trade-off between the development of organs required to obtain resources from the light, and those required for soil resource uptake. Seedlings from one of the populations exhibited a relatively low total dry biomass in drought environment, but showed significantly more resources to water uptake from the soil by investing in fine root growth, at the expense of leaf growth, enhancing their potential for better acclimation to future predicted drought events in the context of global warming. © 2019 Friends Science Publishers

Keywords: Phenotypic plasticity; Adaptive strategy; *Cotinus coggygia*; Drought stress; Functional traits; Intraspecific variation

Introduction

Intraspecific differences are an important component of genetic diversity and adaptability to environmental change (Hajek *et al.*, 2013). Increasing evidence suggests that forest plant species will experience more frequent and severe drought events as a result of global changes in climate (Dai, 2013; Aubin *et al.*, 2016). Determining the variation in acclimation and adaptive patterns that exists within conspecific tree varieties should improve our understanding of how the species responds to water-limiting conditions, and thus to future warmer climate scenarios. Assessing the traits associated with the adaptive responses and quantifying this variation will become increasingly critical to future breeding practices.

Drought acclimation strategy in plants is determined by a variety of functional traits (Blum, 2011; Grossiord *et al.*, 2017) which include the morphological characteristics, such as root morphology (Freschet and Roumet, 2017), that serve as fundamental links between the abiotic environment and organismal fitness (McGill *et al.*, 2006; Violle *et al.*, 2007), as well as drivers for the response of a plant to, and the effect of a plant on, the surrounding environment (*e.g.*, resource availability) (Violle and Jiang, 2009). General patterns in plant functional trait variation under drought stress have emerged from previous studies (Ackerly, 2004; Lloret *et al.*,

2016) that indicate that some leaf and root functional traits (*e.g.*, SLA and SRL), and the linkages between them, may constitute direct proxies of resource acquisition and utilization efficiency when trees are exposed to drought (Poorter and Markesteijn, 2008; Markesteijn and Poorter, 2009; Matías *et al.*, 2012).

Plants deal with environmental variations through phenotypic plasticity (Wang *et al.*, 2017). In response to different moisture environments, phenotypic plasticity of functional traits is the result of shifts in plant function including resource acquisition and utilization (Sánchez-Gómez *et al.*, 2008; Matías *et al.*, 2012). As an example, a drought-induced decrease in specific leaf area enhances the tolerance of leaves to high xylem tension and increases the ability to conserve water (Ennajeh *et al.*, 2010; Anderegg and Hillerislambers, 2016). Water-stressed (WS) plants develop deeper (Tardieu, 2012; Paz *et al.*, 2015) and more ramified (Jaleel *et al.*, 2009; Reich, 2014) roots to ensure access to water and the maintenance of biomass production, **because a high specific root length or specific root surface area optimizes** soil water-uptake area under drought conditions (Poorter and Markesteijn, 2008; Weemstra *et al.*, 2016). Since fine roots form the majority of the length and surface area of the roots, and are also the most active part of the roots in obtaining water (Comas *et al.*, 2013), increased fine root growth in drought environments

leads to an increase in resource acquisition and productivity (Comas *et al.*, 2013; Chiatante *et al.*, 2015). Moreover, the shifts in patterns of biomass allocation by trees between different absorptive organs during a drought reflect the changing priorities and trade-offs for resource acquisition (Weiner, 2004; Brunner *et al.*, 2015).

Some trait-based researches have highlighted patterns of variation in functional traits that may explain plant survival strategies under different environmental conditions (Matfás *et al.*, 2012; Chiatante *et al.*, 2015). Several studies have focused on the intraspecific differences in functional trait responses to water stress in agroforestry systems (Zheng *et al.*, 2010; De *et al.*, 2012; Hajek *et al.*, 2013, 2014; Anderegg and Hillerislambers, 2016; Elazab *et al.*, 2016; Ahrar *et al.*, 2017). However, much remains unanswered, and there is a growing need for more comprehensive research into the roles of functional traits in the adaptive strategies adopted by conspecific trees for maintaining growth and productivity under conditions of water shortage (Hajek *et al.*, 2013). Furthermore, root economics spectrum (RES) is reported to be widely used to interpret plant strategies for resource acquisition and conservation (Miyatani *et al.*, 2018), but there is only a limited understanding of the differences in root trait variation across environmental gradients (Laliberté, 2016), and the fluctuating trade-offs or priority patterns between functional traits in aboveground and belowground organs under drought stress have not been fully explored (Lloret *et al.*, 2016; Pivovarov *et al.*, 2016).

The smoke tree (*Cotinus coggygia*), which is widely used in landscaping due to its vivid leaf color ranging from yellow to orange and brilliant red-purple in autumn, is valued economically for its yellowish wood, yellow dye, tannins, and fragrant oil extractives from its leaves and wood. It is very useful in areas with limited or no irrigation as a consequence of its well adaptation to dry soil (Deng *et al.*, 2016), but suffers growth limitations under low water availability (Li *et al.*, 2014, 2015). Our previous work demonstrated that *C. coggygia* seedlings exhibited large, population-specific differences in root morphology (Li *et al.*, 2014) and leaf gas exchange in response to stress conditions, indicating that there is greater potential for *C. coggygia* to tolerate drought than tree species with less intraspecific variation. These studies provided the groundwork for further research on the adaptability of *C. coggygia* to drought environments and future changes in climate. Moreover, information on whether functional trait plasticity has an influence on the *C. coggygia*'s acclimation to drought is scarce. The present study investigated whether the leaf and fine root functional traits of *C. coggygia* differ in their plasticity in acclimation to water stress. The tested hypothesis was that the shifts in the leaf and fine functional traits could describe the adaptive strategy for tolerating drought in *C. coggygia*. Furthermore, it is expected that the leaf and fine root functional traits vary in response to water regimes and between *C. coggygia* populations. To address these hypotheses, an experiment was designed combining well-

irrigated and water-stressed conditions to compare functional traits related with leaf and fine root morphology (*i.e.*, specific leaf area, leaf area ratio, specific fine root length, fine root length ratio and fine root length/leaf area), functional traits associated with leaf and fine root biomass allocation (leaf biomass fraction, fine root biomass fraction, and fine root bio-mass/leaf biomass), and one functional trait represented plant overall performance (*i.e.*, total dry biomass) in *C. coggygia* seedlings collected from five different locations in Northern China.

Materials and Methods

Seed Collection

Annual seedlings originating in the following five different places were used (Table 1, data source: National Meteorological Information Center, <http://data.cma.cn/>): Yanqing County in Beijing (code: P1), Zhanhuang County of Shijiazhuang City in Hebei Province (code: P2), Gaoxin District of Tai'an City in Shandong Province (code: P3), Jiang County of Yuncheng City in Shanxi Province (code: P4), and Shanzhou District of Sanmenxia City in Henan Province (code: P5). A plot of the locations of the five seed collection sites is presented in Fig. 1. These sites encompass the natural distribution of *C. coggygia* in China. The seedlings were raised from seeds collected from forests in the five regions during the 2013 fruiting period. Any clearly aborted and depredated seeds were rejected, and the remainder were stored at 4°C until the cold-moist stratification treatment.

Study Site, Seedling Cultivation and Treatment

The study was conducted within the Puzhaoyuan Nursery in Jiufeng Experimental Station of Beijing Forestry University, Beijing, China (39°48'N, 110°15'E). This area experiences a semi-humid temperate climate, with cold, dry winters and hot, rainy summers. The mean minimum and maximum temperatures were -19.6°C and 39.7°C, respectively, and the mean annual precipitation was 644 mm yr⁻¹, of which more than 70% occurs between July and September. The soil was sandy alluvial cinnamon, and homogenous across the site, with 700, 5.4, and 180 mg kg⁻¹ of nitrogen, potassium, and phosphorous, respectively, a pH of 7.6, and 1.66–1.96% of organic matter.

In December 2013, the seeds were sterilized by soaking in 0.5% KMnO₄ solution for 30 min, followed by rinsing three times with distilled water. A cold-moist stratification treatment was then performed, in which moist (60% ~ 70% relative humidity) fine sand and seeds (sand/seeds = 3:1, v/v) were buried in soil in the nursery field for approximately three months under natural conditions. Following germination in February 2014, seedlings were planted in trays (one seedling per tray) in a uniform mixture of 75% peat and 25% perlite (v/v). The plants were established in the greenhouse within the nursery with an average air temperature of 19.2°C

Table 1: Location and general climatic conditions of the five seed sources of *C. coggygia* used in this study

Seed source code	Latitude (N)	Longitude (E)	ANP (mm)	GSP (mm)	WMP (mm)	DMP (mm)	ANT (°C)	GST (°C)	WMT (°C)	CMT (°C)
P1	40° 21'	116° 1'	435	427.6	122.5	2.0	9.7	14.7	39.2	-26.2
P2	37° 39'	114° 23'	508.9	497.6	123.2	2.6	13.6	18.2	43.4	-16.2
P3	36° 4'	117° 10'	686.5	664	205.9	5.3	13.3	17.7	42.1	-20.7
P4	35° 29'	111° 34'	573.5	550.5	108.6	6.3	11.9	16.3	39.4	-20.5
P5	34° 43'	111° 6'	549.6	532.1	107.2	4.8	14.4	18.6	41.4	-12.8

Note: ANP: average annual precipitation; GSP: growing season mean precipitation; WMP: precipitation of the wettest month; DMP: precipitation of the driest month; ANT: average annual temperature; GST: growing season mean temperature; WMT: max. temperature of the warmest month; CMT: min. temperature of the coldest month

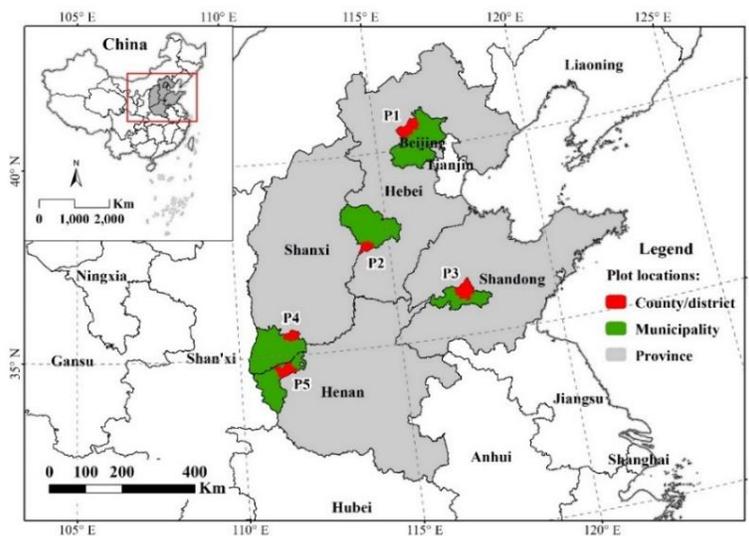


Fig. 1: The distributions of the five seed collection sites in this study. The northern isolated populations of *C. coggygia* were covered in our sampling sites. P1: Yanqing County in Beijing; P2: Zhanhuang County of Shijiazhuang City in Hebei Province; P3: Gaoxin District of Tai'an City in Shandong Province; P4: Jiang County of Yuncheng City in Shanxi Province; P5: Shanzhou District of Sanmenxia City in Henan Province

(range, 14.5–23.9°C), an average relative air humidity of 62.4% (range, 40.6–84.2%) and a daily average photosynthetic photo flux density (PPFD) of $894.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (maximum, $1050.8 \mu\text{mol m}^{-2} \text{s}^{-1}$) with a 12-h day/night cycle. On April 15, 2014, 60-day-old seedlings approximately 10 cm in height were transferred to the study field within the nursery, beneath a rain exclusion shelter constructed from a metal frame supporting a transparent, water-impermeable plastic film (rolled up if no rain occurred). PVC boards were inserted to a depth of 1.5 m along the boundaries of the study field to prevent the inflow of surface water and nutrients between different plots. The seedlings were irrigated to near the soil field water capacity (FWC) at 5 to 7 day intervals for two months. On June 15, all seedlings showed good and homogeneous growth under these conditions: P1: height 32.99 cm, diameter 4.08 mm; P2: height 35.89 cm, diameter 4.54 mm; P3: 32.12 cm, diameter 3.97 mm; P4: height 34.17 cm, diameter 4.15 mm; P5: 33.24 cm, diameter 4.27 mm.

A completely random design was adopted, and a total of 300 seedlings (60 seedlings per population) were randomly assigned to well-irrigated (WI) and water-stressed (WS) treatments at their fast-growing stage between June 15 and September 12, 2014. The soil water content (SWC) of the

two irrigation schemes was set to 75%–85% of FWC (SWC-WI) and 35%–45% of FWC (SWC-WS), respectively. Each treatment was applied to 30 replicates per population (*i.e.*, 150 seedlings per treatment). The total plot size was 24×17 m, and the plot size of each treatment was 17×12 m. The replicated seedlings from each population were randomly assigned to two neighboring rows, with 1.0×1.0 m spacing between the seedlings. The water status of the top 20 cm of the soil was determined by the weighing method every two days. During the 90-day experimental period, the weeds were removed manually to reduce competition and pesticides were applied to limit attack by pests.

Determination of Seedling Functional Traits

Several functional traits were taken for assessment in this study, and the details are provided in Table 2. On September 12, 2014, five 7-month-old seedlings from each population grown under each treatment condition were randomly selected and harvested (Fig. S1). Each plant was partitioned into leaves, stems, coarse roots and fine roots (≤ 2 mm diameter). The fine root samples were separated in a water bath and scanned with a transmitting scanner system (Epson Expression 1680 1.0, Tokyo, Japan).

Table 2: Summary of the functional traits correlated with leaf and fine root morphology, biomass allocation and plant overall performance considered in this study

Traits	Abbreviation	Definition	Functional meaning
Traits Related with Leaf and Fine Root Morphology and Their Linkages			
Specific Leaf Area	SLA (cm ² g ⁻¹)	Leaf Area/Leaf Dry Biomass	Light interception capacity
Leaf Area Ratio	LAR (cm ² g ⁻¹)	Leaf area/Total dry biomass	Photosynthetic area that can support productivity of individual plant
Specific Fine Root Length	SFRL (cm g ⁻¹)	Fine Root Length/Fine Root Biomass	Fine root uptake ability of soil resources
Fine Root Length Ratio	FRLR (cm g ⁻¹)	Fine Root Length/Total Dry Biomass	Fine root length that can support productivity of individual plant
Fine Root Length/Leaf Area	FRL/LA (cm cm ⁻²)	Fine Root Length/Leaf Area	Trade-off between root uptake ability and leaf interception capacity
Traits Related with Leaf and Fine Root Biomass Allocation and Their Linkages			
Leaf Biomass Fraction	LMF (g g ⁻¹)	Leaf Dry Biomass/Total Biomass × 100	Dry Contribution of photosynthesis capacity to plant biomass accumulation
Fine Root Biomass Fraction	FRMF (g g ⁻¹)	Fine Root Dry Biomass/Total Biomass × 100	Dry Contribution of root water and nutrient absorption capacity to plant biomass accumulation
Fine Root Biomass/Leaf Biomass	FR/L (g g ⁻¹)	Fine Root Biomass/Leaf Biomass	Dry Trade-off between leaf and fine root biomass accumulation
Trait Related with Seedling Overall Performance			
Total Dry Biomass	TB (g)	Sum of Leaf, Stem and Root Biomass	Dry Plant productivity

Image analysis of the fine root length (FRL, cm) was conducted using WinRHIZO software (Regent Instruments, Quebec, Canada). Three leaves per seedling selected from the upper, middle and lower part were used for the determination of specific leaf area (SLA, cm² g⁻¹). Leaf area was measured with an Li-3000 leaf area meter (Li-Cor, Inc., Lincoln, NE, USA). Following the above measurements, the leaves, stems, coarse roots, and fine roots of the plants were oven-dried at 70°C until a constant weight (balance to 0.001 g) was achieved, and then weighed. Total leaf area per plant (TLA, cm²) was calculated by multiplying the measured SLA by the total leaf dry biomass.

Data Processing

Analysis of variance: The trait differences across drought treatments and populations were analyzed using analysis of variance (ANOVA). The Turkey Test was used to compare means in subsequent post hoc analysis, and significance was assessed at the significance level $P \leq 0.05$. The values of each functional trait are presented as mean ± standard deviation (SD) throughout this paper. All the statistical analyses were processed in Origin version 9.2.

Relative change: The relative change of each functional trait (Eq.1) caused by drought stress was calculated as:

$$\text{Relative change (\%)} = (FT_{ws} - FT_{wi}) / FT_{wi} \times 100 \quad (1)$$

Where FT_{wi} is the functional trait mean under WI condition; and FT_{ws} is the functional trait mean under WS condition.

Principal component analysis (PCA): In order to assess the distinction of the adaptive patterns in different populations, a principal component analysis (PCA) using the original functional trait data was carried out. The PCA was processed in CANOCO software for windows (Microcomputer Power, Ithaca, NY, USA).

Phenotypic plasticity estimation and linear regression analysis: For the estimation of phenotypic plasticity of each

functional trait (Eq. 2), the Relative Distances Plasticity Index (RDPI) was applied here (Valladares *et al.*, 2006):

$$RDPI = \frac{\sum (d_{ij \rightarrow i'j'} / (x_{i'} + x_{j'}))}{n} \quad (2)$$

Where x is the functional traits; i represents a given level of the drought treatment and j refers to the individual number identification along one drought treatment when the data is considered as a rectangular matrix; i and i' means different individuals grown in different drought treatments, and j and j' means two randomly selected individuals; $d_{ij \rightarrow i'j'}$ was defined as the distance among functional trait values for all pairs of individuals; and n is the total number of distances.

Linear regression was implemented to examine the relationships between the plasticity of total dry biomass associated with seedling overall performance and the plasticity of the other functional traits, and between the plasticity of pairwise leaf and root functional traits (*i.e.*, SLA and SFRL, LAR and FRLR, and LMF and FRMF).

Results

Phenotypic Plasticity of Leaf and Fine Root Functional Traits

The differences in phenotypic plasticity among functional traits were significantly affected by water deficit. The greatest plasticity was observed in FRL/LA, which was significantly higher than the rest of traits except for FRLR. Moreover, SFRL, FR/L, FRMF and LAR were relatively high (Table 3).

Also, significant differences in overall plasticity were noted among populations across all functional traits. In particular, the plasticity of SFRL, FRLR, FRL/LA and TB for P4 were the highest, and the plasticity of SFRL, FRLR and FRL/LA for P4 were significantly higher than the rest of populations, therefore, the overall plasticity in response to

Table 3: Phenotypic plasticity in response to drought stress for each functional traits and populations and the overall plasticity was achieved using the RDPIs index. The capital letters (A to F) indicated differences among the studied traits. The capital letters in italic (A to D) indicated differences in all traits among the populations. The lowercase letters (a to d) indicated differences in one trait among populations. One-way ANOVA was used with Turkey Test at the 0.05 level

Traits	P1	P2	P3	P4	P5	Overall Plasticity of Traits
Traits Related with Leaf and Fine Root Morphology and Their Linkages						
SLA	0.11 a	0.08 b	0.06 b	0.06 b	0.07 b	0.076 G
LAR	0.25 a	0.09 c	0.16 b	0.11 c	0.21 a	0.166 E
SFRL	0.16 c	0.26 b	0.29 b	0.53 a	0.25 bc	0.297 BC
FRLR	0.23 cd	0.44 b	0.16 d	0.72 a	0.26 c	0.361 AB
FRL/LA	0.38 b	0.39 b	0.21 c	0.72 a	0.22 c	0.384 A
Traits Related with Leaf and Fine Root Biomass Allocation and Their Linkages						
LMF	0.15 a	0.07 b	0.11 b	0.07 b	0.18 a	0.116 F
FRMF	0.14 b	0.26 a	0.25 a	0.23 a	0.22 b	0.251 D
FR/L	0.25 bc	0.31 ab	0.36 a	0.35 a	0.19 c	0.291 C
Trait Related with Seedling Overall Performance						
TB	0.06 c	0.12 b	0.17 a	0.19 a	0.09 bc	0.125 F
Overall plasticity of populations	0.192 BC	0.224 B	0.197 BC	0.331 A	0.188 C	

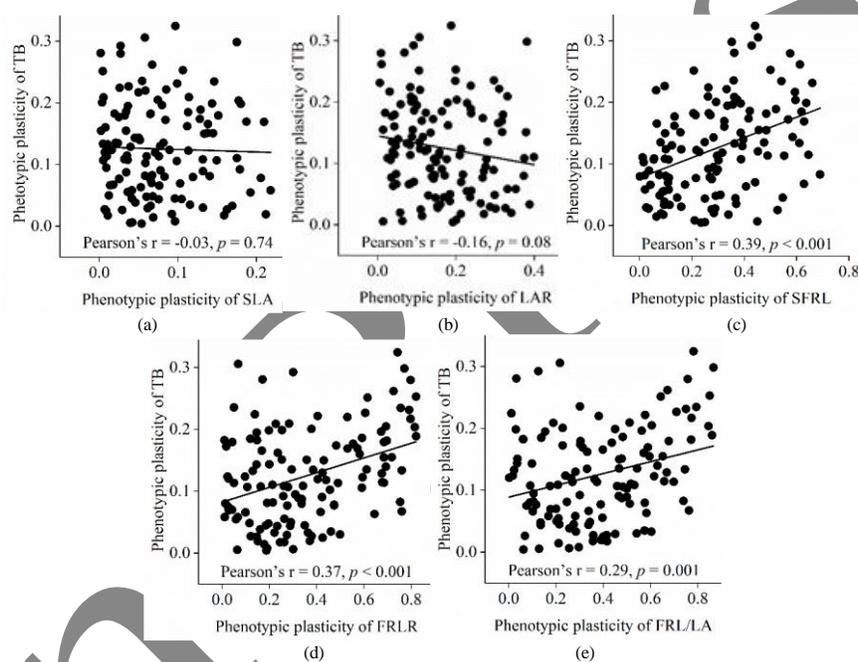


Fig. 2: Linear regression between phenotypic plasticity of seedling overall performance (total dry biomass) and phenotypic plasticity of (a) specific leaf area (SLA); (b) leaf area ratio (LAR); (c) specific fine root length (SFRL); (d) fine root length ratio (FRLR); (e) fine root length/leaf area (FRL/LA)

restricted water for P4 seedlings were observed to be significantly higher than the other four populations, followed by P2, P3, P1 and P5 (Table 3).

Relationships Between Functional Trait Plasticity and Seedling Overall Performance Plasticity

The phenotypic plasticity of TB had a significantly positive relationship with the phenotypic plasticity of FRMF (Fig. 3b), FR/L (Fig. 3c), SFRL (Fig. 2c), FRLR (Fig. 2d) and FRL/LA (Fig. 2e) (the Pearson's r from high to low), while a significantly negative association was observed with the phenotypic plasticity of LMF (Fig. 3a).

Relationships Between Pairwise Leaf and Fine Root Functional Trait Plasticity

The relationships between phenotypic plasticity of pairwise leaf and fine root functional traits were investigated, and a significantly negative correlation was found between the phenotypic plasticity of LAR and FRLR (Fig. 4b).

Influences of Drought Stress and Intraspecific Variation

All functional traits were significantly affected by low soil water content. In general, FRL/LA ($P \leq 0.001$), FRLR ($P \leq 0.001$), FR/L ($P \leq 0.001$), and FRMF ($P \leq 0.001$) were

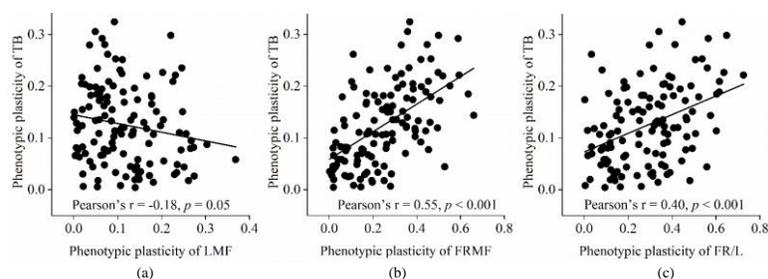


Fig. 3: Linear regression between phenotypic plasticity of seedling overall performance (total dry biomass) and phenotypic plasticity of (a) leaf biomass fraction (LMF); (b) fine root biomass ratio (FRMF); (c) fine root/leaf ratio (FR/L)

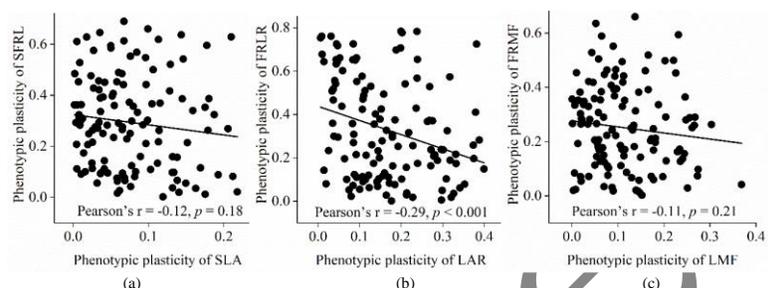


Fig. 4: Linear regression between phenotypic plasticity of (a) specific leaf area (SLA) and specific fine root length (SFRL); (b) leaf area ratio (LAR) and fine root length ratio (FRLR); (c) leaf biomass fraction (LMF) and fine root biomass fraction (FRMF)

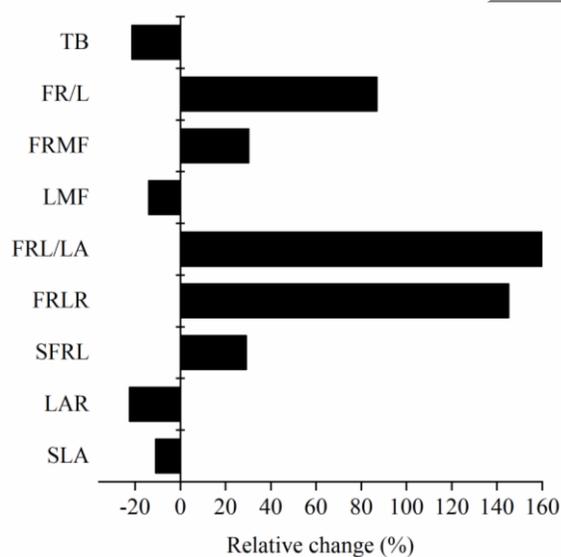


Fig. 5: Relative changes of the tested functional traits under WI and WS treatments. The relative change values are calculated using the functional trait mean under WI condition and WS condition

significantly increased by dropping water content, represented by their relative changes of 168.93%, 145.16%, 86.80% and 30.13%, respectively. While the LAR ($P \leq 0.001$), LMF ($P \leq 0.001$) and SLA ($P = 0.002$) saw a decrease of 22.44%, 13.95% and 10.89%, respectively (Fig. 5).

Significant effects of population were detected in all traits. In response to drought, TB decreased significantly for

all populations but P1. The TB decreasing order under WS condition was $P5 > P2 > P1 > P4 > P3$ (Table 5). SLA values were decreased significantly by water scarcity for P1 and P2 but no significant effects were found for the rest of populations. Drought decreased LAR and LMF significantly only for P1 and P5 and P1 exhibited the lowest LAR and LMF, with no significant differences comparing to P5 (Table 4). Under WS treatment, P4 seedlings exhibited a significantly increase in SFRL, FRLR, FRL/LA, FRMF and FR/L, and exhibited a significantly higher SFRL, FRLR and FRL/LA than the other four populations. P2's SFRL, FRLR and FRMF and P1's FR/L ranked only second to P4. However, for P5 the opposite trends in SFRL, FRLR, FRL/LA and FRMF were observed and values for these traits were the lowest for this population (Table 4 and 5).

Fig. 6a and b visually reflected the adaptive tendencies of the well-watered and water-stressed seedlings from different populations, explaining 60.73% and 78.33% of the total variability, respectively. Seedlings from different populations occupied different positions and displayed different correlations with the functional traits in the population-trait biplots. Particularly, in the drought environment (Fig. 6b), the arrows of FRLR, SFRL, FRL/LA, FRMF, and FR/L were all clustered on the right of the PC1 axis, and remarkably, the angle between the PC1 axis and the arrows of FRLR and FRL/LA was much smaller compared to the well-watered conditions (Fig. 6a). Seedlings from P4, were found on the right-hand side of the PCA, characterized by the highest SFRL, FRLR, FRL/LA, FRMF and FR/L.

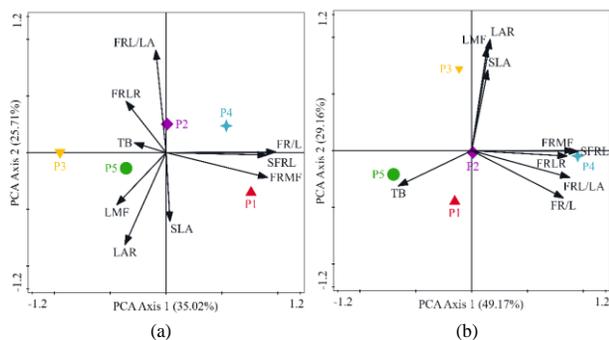


Fig. 6: Distribution of the tested functional traits and the five populations in a Principal Component Analysis (PCA) under WI (a) and WS (b) treatments. P1: up triangle in red; P2: diamond in purple; P3: down triangle; P4: star in blue; P5: circle in green

Discussion

Plasticity in Functional Traits Drives the Adaptive Patterns of *C. coggygria* Seedlings Under WS Conditions

Functional traits are defined either as surrogates of plant function or as these functions, have a strong influence on organismal performance and individual fitness (Violle *et al.*, 2007). Functional trait plasticity may be adaptive, as it permits modulations and adjustments, and changes the nature of interactions between an individual and its environment and thus enables appropriate responses to environmental challenges (Miner *et al.*, 2005; Dai, 2013), for this reason, the close relationship between trait plasticity and plant performance implies that the traits displayed under drought may depend on the ability of a plant to adjust these characteristics (Sánchez-Gómez *et al.*, 2008). In general, a high plasticity in functional traits implies an adaptive advantage when soil resource availability is subject to rapid change (Miner *et al.*, 2005; Hajek *et al.*, 2013).

Our results support these ideas, for instance, FRL/LA, FRLR, SFRL, FR/L and FRMF showed greater phenotypic plasticity (Table 3), and the phenotypic plasticity of these traits had a significantly positive relation with the phenotypic plasticity of TB, while the phenotypic plasticity of SLA, LAR and LMF presented a negative correlation to the phenotypic plasticity of TB, among which only LMF was found to be significant (Fig. 3 and 4), indicating that the plasticity of FRL/LA, FRLR, SFRL, FR/L, FRMF and LMF could be regarded as primary factors determining the plasticity of *C. coggygria*'s overall performance in water-deficit environment.

Furthermore, the coordination between leaf and root functional traits is considered as analogous illustrations of uptake potential (Reich, 2014; Weemstra *et al.*, 2016) when considering the resource trade-off economics between the leaf and the root (Hajek *et al.*, 2013) and links may exist between a high degree of plasticity of one trait and low level of plasticity of other traits (Wang *et al.*, 2017).

Table 4: Mean values and standard deviation (n = 5) for the functional traits related with leaf and fine root morphology across the two drought treatments for each population. The capital letters (A and B) indicated differences between WI and WS treatments and the lowercase letters (a to e) indicated differences among populations. One-way ANOVA was used with Turkey Test at the 0.05 level

Traits	Population	WI	WS
SLA (cm ² g ⁻¹)	P1	163.41 ± 9.21 ^{A(a)}	131.31 ± 15.72 ^{B(a)}
	P2	158.29 ± 19.82 ^{A(a)}	135.18 ± 8.64 ^{B(a)}
	P3	148.42 ± 10.21 ^{A(a)}	144.40 ± 22.22 ^{A(a)}
	P4	154.84 ± 21.80 ^{A(a)}	140.52 ± 8.76 ^{A(a)}
	P5	147.90 ± 26.35 ^{A(a)}	137.74 ± 8.99 ^{A(a)}
LAR (cm ² g ⁻¹)	P1	66.30 ± 9.35 ^{A(ab)}	39.42 ± 6.14 ^{B(b)}
	P2	56.44 ± 11.59 ^{A(b)}	51.42 ± 1.30 ^{A(ab)}
	P3	71.52 ± 4.96 ^{A(a)}	65.07 ± 24.01 ^{A(a)}
	P4	63.06 ± 14.22 ^{A(ab)}	52.66 ± 8.14 ^{A(ab)}
	P5	68.20 ± 10.68 ^{A(ab)}	43.89 ± 5.52 ^{B(b)}
SFRL (cm g ⁻¹)	P1	66.37 ± 20.94 ^{A(b)}	87.15 ± 13.83 ^{A(b)}
	P2	81.36 ± 42.31 ^{A(b)}	105.01 ± 44.23 ^{A(b)}
	P3	141.74 ± 34.10 ^{A(a)}	77.56 ± 20.93 ^{B(b)}
	P4	82.08 ± 33.21 ^{B(b)}	264.32 ± 57.35 ^{A(a)}
	P5	90.70 ± 31.36 ^{A(b)}	62.80 ± 21.51 ^{A(b)}
FRLR (cm g ⁻¹)	P1	10.94 ± 2.25 ^{B(ab)}	17.42 ± 3.27 ^{A(b)}
	P2	9.03 ± 2.19 ^{B(b)}	25.00 ± 9.15 ^{A(b)}
	P3	14.23 ± 4.09 ^{A(a)}	15.30 ± 5.47 ^{A(b)}
	P4	12.25 ± 3.41 ^{B(ab)}	76.04 ± 12.12 ^{A(a)}
	P5	11.70 ± 2.86 ^{A(ab)}	8.81 ± 4.87 ^{A(b)}
FRL/LA (cm cm ⁻²)	P1	0.20 ± 0.03 ^{B(a)}	0.46 ± 0.14 ^{A(b)}
	P2	0.20 ± 0.07 ^{B(a)}	0.48 ± 0.17 ^{A(b)}
	P3	0.23 ± 0.07 ^{A(a)}	0.28 ± 0.21 ^{A(bc)}
	P4	0.24 ± 0.09 ^{B(a)}	1.46 ± 0.25 ^{A(a)}
	P5	0.20 ± 0.05 ^{A(a)}	0.20 ± 0.12 ^{A(c)}

Table 5: Mean values and standard deviation (n = 5) for the functional traits related with biomass allocation and overall performance across the two drought treatments for each population. The capital letters (A and B) indicated differences between WI and WS treatments and the lowercase letters (a to e) indicated differences among populations. One-way ANOVA was used with Turkey Test at the 0.05 level

Traits	Population	WI	WS
LMF (g g ⁻¹)	P1	40.53 ± 4.83 ^{A(bc)}	30.07 ± 3.47 ^{B(c)}
	P2	35.59 ± 5.46 ^{A(c)}	38.18 ± 2.93 ^{A(b)}
	P3	48.24 ± 2.59 ^{A(a)}	43.99 ± 10.50 ^{A(ab)}
	P4	40.48 ± 4.63 ^{A(bc)}	37.46 ± 5.41 ^{A(bc)}
	P5	46.42 ± 5.45 ^{A(ab)}	32.10 ± 4.80 ^{B(c)}
FRMF (g g ⁻¹)	P1	17.41 ± 4.09 ^{A(a)}	20.49 ± 5.31 ^{A(bc)}
	P2	12.20 ± 2.93 ^{B(b)}	25.28 ± 7.40 ^{A(ab)}
	P3	10.32 ± 2.80 ^{B(b)}	20.36 ± 6.64 ^{A(bc)}
	P4	15.79 ± 4.10 ^{B(a)}	29.66 ± 6.48 ^{A(a)}
	P5	13.76 ± 3.71 ^{A(ab)}	13.63 ± 3.55 ^{A(c)}
FR/L (g g ⁻¹)	P1	0.44 ± 0.13 ^{A(a)}	0.70 ± 0.24 ^{A(ab)}
	P2	0.34 ± 0.08 ^{B(ab)}	0.66 ± 0.19 ^{A(ab)}
	P3	0.21 ± 0.06 ^{B(c)}	0.48 ± 0.20 ^{A(b)}
	P4	0.40 ± 0.12 ^{B(ab)}	0.88 ± 0.33 ^{A(a)}
	P5	0.29 ± 0.05 ^{B(bc)}	0.43 ± 0.11 ^{A(b)}
TB (g)	P1	52.68 ± 3.95 ^{A(b)}	47.43 ± 4.46 ^{A(c)}
	P2	69.92 ± 5.40 ^{A(a)}	55.23 ± 4.67 ^{B(b)}
	P3	54.93 ± 5.91 ^{A(b)}	39.28 ± 5.07 ^{B(d)}
	P4	59.38 ± 7.18 ^{A(b)}	40.02 ± 3.60 ^{B(d)}
	P5	72.82 ± 10.59 ^{A(a)}	61.35 ± 2.17 ^{B(a)}

Here, the phenotypic plasticity of LAR and FRLR (Fig. 4b) was observed to have a significantly negative link. This result indicated that the low water availability triggered a shift in the function from leaf to fine root, especially a shift from

enhancing leaf light absorption to strengthening fine root water capture to maximize water foraging. Relations between the plasticity of leaf and fine root morphology traits such as LAR and FRLR, may be used to explain the functionally adaptive tendency of *C. coggygia* seedlings.

Functional Traits in *C. coggygia* Seedlings Vary with Soil Water Availability and Population

The significant decline in SLA and LAR in the seedlings from the five populations following water restriction was observed (Fig. 5; Table 4). This may be explained by light resource interception, as decreased leaf area is one means by which a plant may reduce light absorption and photosynthetic rate (Jaleel *et al.*, 2009). A LAR reduction was the consequence of drought effects on SLA and LMF (Romero-Munar *et al.*, 2018) and the decrease in LAR was higher than LMF (Fig. 5), indicating that the LAR decrease was caused by the SLA decline under drought treatment. A SLA decrease in response to drought reduces water turgor loss, diminishes intrinsic water loss (Chaves *et al.*, 2003) and improves water use efficiency and seedlings' drought resistance (Ackerly, 2004; Anderegg and Hillerislambers, 2016; Chirino *et al.*, 2017).

These findings may also be explained by resource uptake from the soil. In dry environments, trees apportion greater resources to structures that harness the most limiting resource and maximize their root length to optimize water intake (Weiner, 2004; Markesteijn and Poorter, 2009). When roots sense water shortage, the increase in the proliferation of fine roots may compensate effectively for root shrinkage, thereby leading to an increased absorptive surface area of the roots interacting with the soil (Weemstra *et al.*, 2016). SFRL and FRLR are reflections of fine root absorptive area per unit biomass, and the increases are expected to be directly linked to growth in the rate of resource acquisition from the soil (Laliberté, 2016; Weemstra *et al.*, 2016). As hypothesized, the WS *C. coggygia* seedlings showed a preference for a significantly higher SFRL and FRLR (Fig. 5; Tables 4). In addition, FRLR was the trait that showed the greatest variation and relative increase (Fig. 5 and 6). Therefore, developing more fine roots may be a good way to enhance water acquisition and promote water acquisition efficiency for the WS *C. coggygia* seedlings (Comas *et al.*, 2013; Miyatani *et al.*, 2018).

Plant functional trait values linked to biomass accumulation and allocation serve as an accurate quantitative tool to track and describe strategies for resource use and carbohydrate storage in trees (Violle and Jiang, 2009; Aubin *et al.*, 2016). A high belowground biomass fraction contributes to reducing the demand for water (Sánchez-Gómez *et al.*, 2008) and allows for the rapid resumption of root growth (Chiatante *et al.*, 2015). And a significant increase in FRMF was found but a significant decrease in LMF in *C. coggygia* seedlings grown in the water-deficient environment (Fig. 5).

The balance of resource-utilization and resource-allocation strategies between aboveground and belowground organs as soil water content drops, as evidence for a trade-off between leaf and fine root, and a priority for partitioning resources into fine root when water became the most important restriction, because there was a significant increase in FRL/LA and FR/L in stressed seedlings (Fig. 5), suggesting that plants invest more of their assimilated resources into fine roots to ensure water exploration and absorption (Poorter and Markesteijn, 2008; Brunner *et al.*, 2015).

Overall, a conservative strategy (*i.e.*, a water saver strategy, more expensive root tissue investment and lower aboveground biomass allocation) (Chirino *et al.*, 2017) may be *C. coggygia*'s best survival strategy under dry conditions.

As different *C. coggygia* populations have acclimatized themselves to local climate for a long term, they showed distinct responses to the two water treatments (Fig. 3, Table 3 and 5), implying that individuals may utilize a wide range of morphological or physiological adaptations in their leaves and roots to allow them to maintain themselves under drought stress (Ennajeh *et al.*, 2010; Aubin *et al.*, 2016). This potential for functional trait differentiation within a tree species is very crucial for its adaptive evolution (Hajek *et al.*, 2013; Anderegg and Hillerislambers, 2016). Here, we suggested P4 seedlings, although they didn't perform well in TB, **were able to maintain** an effective soil resource use pattern and trade-off mode between aboveground and belowground parts through establishing a developed water- and nutrient-uptake system and investing more assimilates in it. This is supported by their highest SFRL, FRLR, FRL/LA, FRMF and FR/L in response to water stress.

Conclusions

Based on observation of leaf and fine root functional trait phenotypic plasticity during the course of soil drying, it was found that *C. coggygia* seedlings were able to acclimatize to water stress through a conservative strategy by stimulating fine root growth (*i.e.*, higher SFRL, FRLR, and FRMF) and by shifting resource investment from leaf to fine root (*i.e.*, higher FRL/LA and FR/L) to improve root foraging ability, and the considerable intraspecific functional trait differences were also distinguished in *C. coggygia* (*e.g.*, the seedlings from P4 constituted the most effective soil resource-use pattern of the five tested groups), indicating that *C. coggygia* will adopt a flexible strategy and adapt accordingly when it is subjected to drought. Therefore, it can be concluded that the *C. coggygia* species is highly suitable for ongoing climatic change, in particular on landscape sites that become too dry for other ornamental tree species. And *C. coggygia* seed material origin in tree management practices in arid or semiarid zones is worthy of special attention.

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References

- Ackerly, D., 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol. Monogr.*, 74: 25–44
- Ahrar, M., D. Doneva, M. Tattini, C. Brunetti, A. Gori, M. Rodeghiero, G. Wohlfahrt, F. Biasioli, C. Varotto, F. Loreto and V. Velikova, 2017. Phenotypic differences determine drought stress responses in ecotypes of *Arundo donax* adapted to different environments. *J. Exp. Bot.*, 68: 2439–2451
- Anderegg, L.D.L. and J. Hillerislambers, 2016. Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Glob. Change Biol.*, 22: 1029–1045
- Aubin, I., A.D. Munson, F. Cardou, P.J. Burton, N. Isabel, J.H. Pedlar, A. Paquette, A.R. Taylor, S. Delagrange, H. Kebli, C. Messier, B. Shipley, F. Valladares, J. Kattge, L. Boisvert-Marsh and D. McKenney, 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environ. Rev.*, 24: 1–23
- Blum, A., 2011. Drought resistance – is it really a complex trait? *Funct. Plant Biol.*, 38: 753–757
- Brunner, I., C. Herzog, M.A. Dawes, M. Arend and C. Sperisen, 2015. How tree roots respond to drought. *Front. Plant Sci.*, 6: 547
- Chaves, M.M., O.P. Maroco and O.S. Pereira, 2003. Understanding plant responses to drought – from genes to the whole plant. *Funct. Plant Biol.*, 30: 239–264
- Chiatante, D., R. Tognetti, G.S. Scipia, T. Congiu, B. Baesso, M. Terzaghi and A. Montagnoli, 2015. Interspecific variation in functional traits of oak seedlings (*Quercus ilex*, *Quercus trojana*, *Quercus virgiliana*) grown under artificial drought and fire conditions. *J. Plant Res.*, 128: 1–17
- Chirino, E., S. Ruiz-Yanetti, A. Vilagrosa, X. Mera, M. Espinoza and P. Lozano, 2017. Morpho-functional traits and plant response to drought conditions in seedlings of six native species of Ecuadorian Ecosystems. *Flora*, 233: 58–67
- Comas, L.H., S.R. Becker, V.M.V. Cruz, P.F. Byrne and D.A. Dierig, 2013. Root traits contributing to plant productivity under drought. *Front. Plant Sci.*, 4: 442
- Dai, A., 2013. Increasing drought under global warming in observations and models. *Nat. Climate Change*, 3: 52–58
- De, M.M., D. Sánchezgómez, M.T. Cervera and I. Aranda, 2012. Functional and genetic characterization of gas exchange and intrinsic water use efficiency in a full-sib family of *Pinus pinaster* Ait. in response to drought. *Tree Physiol.*, 32: 94–103
- Deng, Z.J., X.F. Hu, X.R. Ai, L. Yao, S.M. Deng, X. Pu and S.Q. Song, 2016. Dormancy release of *Cotinus coggygria*, seeds under a pre-cold moist stratification: an endogenous abscisic acid/gibberellic acid and comparative proteomic analysis. *New Forest.*, 47: 105–118
- Elazab, A., M.D. Serret and J.L. Araus, 2016. Interactive effect of water and nitrogen regimes on plant growth, root traits and water status of old and modern durum wheat genotypes. *Planta*, 244: 125–144
- Ennajeh, M., A.M. Vadel, H. Cochard and H. Khemira, 2010. Comparative impacts of water stress on the leaf anatomy of a drought-resistant and a drought-sensitive olive cultivar. *J. Hort. Sci. Biotech.*, 85: 289–294
- Freschet, G.T. and C. Roumet, 2017. Sampling roots to capture plant and soil functions. *Funct. Ecol.*, 31: 1506–1518
- Grossiord, C., S. Sevanto, H.D. Adam, A.D. Collins, L.T. Dickman, N. McBranch, S.T. Michanletz, E.A. Stockton, M. Vigil and N.G. McDowell, 2017. Precipitation, not air temperature, drives functional responses of trees in semi-arid ecosystems. *J. Ecol.*, 105: 163–175
- Hajek, P., D. Hertel and C. Leuschner, 2013. Intraspecific variation in root and leaf traits and leaf-root trait linkages in eight aspen demes (*Populus tremula* and *P. tremuloides*). *Front. Plant Sci.*, 4: 415
- Hajek, P., C. Leuschner, D. Hertel, S. Delzon and B. Schuldt, 2014. Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*. *Tree Physiol.*, 34: 744–756
- Jaleel, C.A., P. Manivannan, A. Wahid, M. Farooq, H.J. Al-juburi, R. Somasundaram and R. Panneerselvam, 2009. Drought stress in plants: a review on morphological characteristics and pigments composition. *Intl. J. Agric. Biol.*, 11: 100–105
- Laliberté, E., 2016. Below-ground frontiers in trait-based plant ecology. *New Phytol.*, 213: 1597–1603
- Li, J.H., X.H. Qi, C.Y. Xu and Y.M. Wang, 2014. Short-term responses of root morphology to drought stress of *Cotinus coggygria* seedlings from four varied locations in northern China. *J. Beijing For. U.*, 36: 48–54
- Li, J.H., X.H. Qi, C.Y. Xu, C. Wang, H.X. Liu and P. Sun, 2015. Short-term responses of leaf gas exchange characteristics to drought stress of *Cotinus coggygria* Seedlings. *Sci. Silvae Sin.*, 51: 29–41
- Lloret, F., E.G.D.L. Riva, I.M. Pérez-Ramos, T. Marañón, S. Saura-Mas, R. Díaz-Delgado and R. Villar, 2016. Climatic events inducing die-off in Mediterranean shrublands: are species' responses related to their functional traits? *Oecologia*, 180: 961–973
- Markesteyn, L. and L. Poorter, 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J. Ecol.*, 97: 311–325
- Mattas, L., J.L. Quero, R. Zamora and J. Castro, 2012. Evidence for plant traits driving specific drought resistance. A community field experiment. *Exp. Bot.*, 81: 55–61
- Mcgill, B.J., B.J. Enquist, E. Weiher and M. Westoby, 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21: 178–185
- Miner, B.G., S.E. Sultan, S.G. Morgan, D.K. Padilla and R.A. Relyea, 2005. Ecological consequences of phenotypic plasticity. *Trends Ecol. Evol.*, 20: 685–692
- Miyatani, K., T. Tanikawa, N. Makita and Y. Hirano, 2018. Relationships between specific root length and respiration rate of fine roots across stands and seasons in *Chamaecyparis obtusa*. *Plant Soil*, 423: 215–227
- Paz, H., F. Pineda-García and L.F. Pinzón-Pérez, 2015. Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia*, 179: 551–561
- Pivovarov, A.L., S.C. Pasquini, M.E.D. Guzman, K.P. Alstad, J.S. Stemke and L.S. Santiago, 2016. Multiple strategies for drought survival among woody plant species. *Funct. Ecol.*, 30: 517–526
- Poorter, L. and L. Markesteyn, 2008. Seedling traits determine drought tolerance of tropical tree species. *Biotropica*, 40: 321–331
- Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.*, 102: 275–301
- Romero-Munar, A., E. Baraza, J. Cifre, C. Achir and J. Gullás, 2018. Leaf plasticity and stomatal regulation determines the ability of *Arundo donax* plantlets to cope with water stress. *Photosynth.*, 56: 698–706
- Sánchez-Gómez, D., M.A. Zavala and F. Valladares, 2008. Functional traits and plasticity linked to seedlings' performance under shade and drought in Mediterranean woody species. *Ann. For. Sci.*, 65: 311
- Tardieu, F., 2012. Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario. *J. Exp. Bot.*, 63: 25–31
- Valladares, F., D. Sanchez-Gomez and M.A. Zavala, 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *J. Plant Ecol.*, 94: 1103–1116
- Violle, C. and L. Jiang, 2009. Towards a trait-based quantification of species niche. *J. Plant Ecol.*, 2: 87–93
- Violle, C., M.L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel and E. Garnier, 2007. Let the concept of trait be functional! *Oikos*, 116: 882–892

Wang, S., R.M. Callaway, D.W. Zhou and J. Weiner, 2017. Experience of inundation or drought alters the responses of plants to subsequent water conditions. *J. Ecol.*, 105: 176–187

Weemstra, M., L. Mommer, E.J.W. Visser, J. Ruijven, T.W. Kuyper, G.M.J.

Mohren and F.J. Sterck, 2016. Towards a multidimensional root trait framework: a tree root review. *New Phytol.*, 211: 1159–1169

Weiner, J., 2004. Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol.*, 6: 207–215

Zheng, Y.X., J.C. Wu, F.L. Cao and Y.P. Zhang, 2010. Effects of water stress on photosynthetic activity, dry mass partitioning and some associated metabolic changes in four provenances of neem (*Azadirachta indica* A. Juss). *Photosynth.*, 48: 361–369

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