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Heritability of early growth traits and their plasticity in 14 woody species of Chinese subtropical forest

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Abstract

Aims
Genetic variation in plant traits represents the raw material for future adaptive evolution. Its extent can be estimated as heritability based on the performance of experimental plants of known relatedness, such as maternal half-sib seed families. While there is considerable heritability information for herbaceous plants and commercially important trees, little is known for woody species of natural subtropical forest. Moreover, it is open whether heritability is higher for species with r- or K-strategies, for more common species with larger distribution ranges than for rarer ones, or for populations closer to the centres of distributional ranges.

Methods
For 14 woody species in Chinese subtropical forest, we collected 13–38 maternal seed families, assessed seed size, grew replicates of each seed family in one more and one less benign nursery environment and measured stem diameter and plant height after 7 months.

Important findings
For the different species, plants grew 1.8–8.1 times taller in the more benign environment. For all 14 species, variation between seed families (and thus heritability) was significant (with very few exceptions at the $P < 0.001$ level) for seed size and for stem diameter and plant height in both nurseries. Moreover, significant seed family by nursery interactions for stem diameter and plant height for all species ($P < 0.001$) indicated significant heritability for plasticity in these traits. Multiple regression analysis suggests that heritabilities were higher for species with higher age at reproduction and higher wood density (traits indicating a K strategy) but also for species with higher specific leaf area (a trait rather indicating an r strategy). Furthermore, heritabilities were higher for species with larger range sizes, while there was no significant relationship between heritabilities and the distance of the study area to the range margins of our study species. In conclusion, the detected large heritability estimates suggest considerable potential for the evolution of plant performance and its plasticity for trees of subtropical forest. Moreover, our study shows that the simple method of comparing plants of different maternal seed families is valuable to address evolutionary ecological questions for so far understudied species.

Keywords: heritability, plant performance, phenotypic plasticity, subtropical forest

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INTRODUCTION

Heritable genetic variation in plant traits represents the raw material for future adaptive evolution. Accordingly, the contribution of heritable genetic variation to total phenotypic variation is essential for evolutionary ecology. Its importance rises even more under global change, as it is unclear to which degree terrestrial plant species are able to adapt to different habitat quality (Billington and Pelham 1991; Blows and Hoffmann 2005; Ensslin and Fischer 2015; Jump and

Penuelas 2005; Savolainen *et al.* 2004). In addition to the heritability of mean traits, future phenotypic variation also very much depends on the heritability of phenotypic plasticity (Bradshaw 1965; Pemac and Tucic 1998; Scheiner 1993; Schlichting 1986; Stearns 1992). While there is considerable heritability information for herbaceous plants (Fischer *et al.* 2004; Fornoni *et al.* 2003; Kelly 1993) and commercially important trees (Dvorak *et al.* 2007; Perfectti and Camacho 1999; Stevens and Lindroth 2005), little is known on genetic variation for woody species of natural stands, especially in subtropical and tropical forest.

Heritability might differ between environments (Johnson and Frey 1967; Hoffmann and Merilä 1999). It might be argued that more heritable variation is expressed in more benign environments, if plants benefit from benign environments in a more uniform manner, thus reducing the environmental contribution to phenotypic variation relative to the contribution due to genetic variation. Alternatively, if poor conditions lead to more uniformly poorer performance, heritability may be higher in more stressful environments.

Many studies on heritability focus on the intraspecific genetic variation of particular target species (Barbour *et al.* 2009; Court-Picon *et al.* 2004; Whitham *et al.* 2003). However, studying individual species does not allow for addressing differences among species with different life histories or with differently sized distribution areas, which may very well lead to differences in heritability (Falconer 1989; Fischer and Van Kleunen 2001). It has been suggested and shown by meta-analysis of isozyme studies that species with pioneer attributes, the so-called r-strategists, may have large genetic variation between, but small genetic variation within, populations, whereas climax attributes may be associated with low genetic diversity between, but high diversity within populations (Hamrick and Godt 1996). Traits distinguishing pioneer from climax tree species, i.e. r- from K-strategists, meaning traits potentially affecting differences in genetic variation between species, may be characterized by lower age at reproduction, less dense wood or higher specific leaf area, as reported for subtropical and tropical trees (Burley *et al.* 2011; Liu *et al.* 2011). Moreover, it may be expected that populations of species with larger distribution ranges have higher genetic variation, as shown by meta-analysis of isozyme studies Gitzendanner and Soltis 2000). Furthermore, populations closer to the centre of species distribution may have higher genetic variation than populations at the margin, as shown for shrub, tree and herb species (Dlugosch and Parker 2008; Mao and Wang 2011; van Kleunen and Fischer 2008). However, differences in genetic variation between species of different strategy or distribution have not been addressed in multispecies studies assessing heritabilities and not for subtropical trees.

Heritable genetic variation can be estimated based on the performance of experimental plants of different degrees of relatedness, such as between and within maternal half-sib seed families. At the same time, such an experimental setting will reveal genetic variation for plasticity, if seed families respond differently to differences between test environments (Scheiner and Lyman 1989).

We studied genetic variation and plasticity of seed size, early stem diameter and sapling height in 14 woody species of Chinese subtropical forest. These traits were selected as they are important performance traits during early growth. We collected 13–38 seed families of these 14 species in the wild, assessed seed size, grew replicates of each seed family in one more benign and one more stressful nursery environment and measured stem diameter and plant height after 7 months of growth. This served to address the following questions: Are heritability in the performance traits seed size and plant size, and heritability of plasticity in plant size rather the rule or the exception across species and environments? Is heritability higher for species with traits rather indicating a K-strategy than for species with traits rather suggesting an r-strategy? Is heritability higher for species with wider distribution ranges and closer to the centres of distribution ranges?

MATERIALS AND METHODS

Species and their characteristics

We selected 14 tree and shrub species of subtropical broad-leaved forest representing different growth forms and distribution ranges (Table 1). Species traits were generation time (minimum age at first reproduction from Zheng (2005) and local expert knowledge (Fang Teng, Gutianshan National Park, Zhejiang, China, personal communication)), growth strategy (evergreen or deciduous), specific leaf area (SLA; from Kröber *et al.* (2012)) and mean core wood density (unpublished data of Martin Böhnke, Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany).

Distribution data for the studied species were compiled from all available data sources. This included specimen location data as obtained from the Global Biodiversity Information Facility (GBIF 2010) and the Chinese Virtual Herbarium (CVH 2010). Moreover, published distribution range maps (Kurata 1964–1973; Horikawa 1972–1976; Menitsky 2005) were geo-referenced and digitized using ArcMap (ESRI). Additionally, geographic information system data sets of county occurrence data for China were obtained from Fang *et al.* (2010). All distribution data were compiled, transformed and analysed within ArcGIS 9.3 (ESRI 2009). Finally, recording localities for SE Asia as listed in Aubréville (1960–1996) and Soepadmo *et al.* (Soepadmo and Wong 1995; Soepadmo *et al.* 1998, 2002, 2004, 2007; Soepadmo and Saw 2000) were geo-referenced using web-based gazetteers (Global Gazetteer 2.2, 2010; NGA GEOnet Names Server, 2010). This allowed us to determine geographic range size as the number of populated 0.25 × 0.25 decimal degree grid cells for each species.

Current climatic attributes at the occurrence locations were obtained for 19 bioclimatic variables measuring temperature and precipitation from the WorldClim 1.4 database (Hijmans *et al.*, 2005; available at: http://www.worldclim.org/) using the extract

Table 1: Characteristics of the 14 studied tree species from subtropical China

Species	Code	Evergreen deciduous	Reproductive age (years)	Wood density (g /cm^3)	Specific leaf area (mm^2/mg)	Range size	Marginality
Ardisia crenata	Ac	E	3	0.55	11.52	1084	0.40
Alniphyllum fortunei	Af	D	6	0.51	15.85	575	0.12
Cinnamomum camphora	Cc	E	8	0.56	11.49	954	0.07
Castanopsis eyrei	Ce	E	15	0.59	9.07	502	0.02
Castanopsis fargesii	Cf	E	15	0.65	8.77	561	0.05
Castanopsis sclerophylla	Cs	E	15	0.57	7.56	359	0.11
Cyclobalanopsis glauca	Cg	E	15	0.74	10.46	996	0.07
Daphniphyllum oldhamii	Do	E	15	0.59	11.64	664	0.06
Eurya muricata	Em	E	3	0.72	8.36	403	0.00
Idesia polycarpa	Ip	D	10	0.47	10.59	668	0.24
Lithocarpus glaber	Lg	E	15	0.67	9.26	554	0.29
Machilus thunbergii	Mt	E	15	0.61	9.74	577	0.42
Rhaphiolepis indica	Ri	E	5	0.85	9.85	467	0.08
Syzygium buxifolium	Sb	E	5	0.80	9.92	500	0.10

Range size is given as the number of raster cells (2.5 arc-min per cell; see Methods). Reproductive age is the minimum age at first reproduction (see Methods).

values by points function in diva-gis 7.3.0 (Hijmans *et al.* 2001) at a spatial resolution of 2.5 arc-min (0.25′ × 0.25′ grid cells).

Climatic niche marginality was determined as an index ranging from 0 for the centre of the climatic niche of species to 1 at the very edge. This was done using a multivariate coinertia analysis (Dolédec *et al.* 2000) quantifying the species-specific niche space along the principal components of the climate data space of all considered species. Then the species-specific local climatic niche marginality was calculated as the mean of the principal component distances between the climatic conditions at the site of the study to the mean conditions across the species range.

Seed sampling

For each species, seeds were collected either in the Gutianshan National Nature Reserve, Zhejiang Province (29°10′19″N, 118°03′50″E), or in forests near Dexing, Jiangxi Province (28°56′47″N, 117°34′43″E) in 2008. These locations are typical for species-rich Chinese mixed broad-leaved forests dominated by evergreen species (Bruelheide *et al.* 2011; Yu *et al.* 2001). For each species, seeds were collected from many fruits of 13 to 38 maternal trees in autumn 2008. Below we refer to offspring from the same maternal tree as maternal seed family or seed family in short. To preserve the vitality of the seeds, we mixed the seed families with plant ash and kept them moist but well aerated over winter 2008–2009.

Cultivation

In April 2009, seeds of all seed families of 12 species were raised in two local commercial nurseries, located in Dexing (D) (28°5′13″N, 117°35′47″E) and Shitiangang (S) (29°08′44″N, 117°57′17″E), and seeds of seed families of *Ardisia crenata* and of *Eurya muricata* only in Dexing. Within each nursery, seeds of each seed family were partitioned into two parts and sown in different blocks for space reasons. In the two nurseries, seeds and seedlings were treated according to two different, locally well-practised methods. In Dexing, seeds were sown in breeding bags (5 cm diameter × 10 cm in height) filled with a mixture of chaff, sawdust, plant ash and fertilizer. Seeds germinated in a greenhouse. Seedlings received occasional nitrogen fertilization, were watered every second day, leaves were sprayed regularly with potassium permanganate for sterilization of pathogenic or parasitic material and pots were weeded. In Shitiangang, seeds were sown in plastic pots (10 cm × 10 cm), filled with local mineral soil mixed with fertilizer and were kept outdoor under plastic shading nets. After germination, seedlings received spray fertilization once and were watered every day. Insecticide and fungicide were applied and weeds removed twice per month. Of the two nursery environments, the greenhouse environment in Dexing was more favourable for germination and plant growth (see Results).

Measurement of quantitative traits

For the seed families of nine species, we assessed seed size as projected area on 350 dpi scans analysed with the software WinSEEDLE 98 (Regent Instruments, Canada).

To measure the size of 7-month-old seedlings for 12 species, we randomly chose 30 individuals per block, species and seed family per nursery and measured their stem height and basal stem diameter.

Data analysis

We estimated the narrow-sense heritability (h^2) of seed area, deduced from one-way analysis of variance (ANOVA; Lynch and Walsh 1998) as $h_1^2 = 4\sigma_s^2/(\sigma_s^2 + \sigma_e^2)$, assuming a sibship coefficient of 1/4 between seed families as for half-sibs, with σ_s^2, the variance component due to differences among seed families and σ_e^2, the residual variance (Falconer 1989). As seeds were derived from many different fruits per tree, we consider the half-sib level as the most likely degree of relatedness within seed families.

The estimates for heritability of tree height and diameter within each nursery were calculated from random model ANOVAs (Lynch and Walsh 1998), in which we regarded block as a random factor, as $h_2^2 = 4\sigma_s^2/(\sigma_s^2+\sigma_i^2+\sigma_e^2)$, with σ_i^2 the variance component of the seed family-by-block interaction. A combined measure ($h^2_{2\_mean}$) was calculated as the mean of h_2^2 for the two nurseries.

As alternative combined measure of heritability of mean traits across the two nurseries, h_3^2 was calculated from mixed model ANOVAs in which we regard nursery as a fixed factor with the same formula $h_3^2 = 4\sigma_s^2/(\sigma_s^2+\sigma_i^2+\sigma_e^2)$ as h_2^2, however with σ_i^2 representing the variance component of the seed family-by-nursery interaction. As we had two blocks in each nursery, we combined the data from one block in Dexing with one block in Shitiangang, calculated h_3^2 for all nursery-by-block combinations and calculated the mean heritability of all possible combinations. As estimate of the heritability of phenotypic plasticity in response to the two nursery environments, we used $h_4^2 = 4\sigma_i^2/\left(\sigma_s^2+\sigma_i^2+\sigma_e^2\right)$ (Scheiner and Lyman 1989). As above, we calculated h_4^2 for all nursery-by-block combinations and used the mean as our final estimate of the heritability of plasticity.

The mean of all seedling heritabilities (h^2_{all}, the mean value for h_2^2, h_3^2 and h_4^2) was also calculated for height and diameter, respectively.

Subsequently, the heritability measures were related to species characteristics by linear regressions. The full model included reproductive age, wood density, SLA, marginality and range site and was reduced stepwise by excluding the least significant terms to arrive at a best final model according to highest statistical significance of remaining terms. All analyses were performed with R v.2.13.1 (R Development Core Team 2011).

RESULTS

Plant size

Seedlings grew much better in the Dexing nursery than in the Shitiangang nursery (Fig. 1). On average, plants grew about three times taller in Dexing than in Shitiangang (range from 1.8 to 8.1; Fig. 1). This was especially obvious for the deciduous species, e.g. *Alniphyllum fortunei* was eight times taller in Dexing than in Shitiangang (mean height 38.6 cm in Dexing vs. 4.8 cm in Shitiangang), and *Idesia polycarpa* was more than five times taller in Dexing than in Shitiangang (28.8 cm in Dexin vs. 5.1 cm in Shitiangang). Mean stem diameter was about one and a half times higher in Dexing than in Shitiangang (range from 1.1 to 2.2; Fig. 1). Among species, differences in diameter and height between the nurseries were highly correlated with each other ($n = 12$; $r = 0.69$, $P = 0.018$).

Heritability

With very few exceptions, the variance components of seed family and of the seed family by nursery interaction (and thus our measures of heritability) were significant for all species at the $P < 0.001$ level (Table 2). Exceptions were lower significance of the heritability h_3^2 for diameter across nurseries for one species (*Cinnamomum camphora*) and the heritability of plasticity h_4^2 for height for *Idesia polycarpa* and for diameter of *Machilus thunbergii* and *Castanopsis eyrei*. The heritabilities of seed area were much larger than the heritabilities of seedling traits (Table 2). Among the study species, the heritabilities of plant height were larger than those for diameter (paired *t*-test, $P < 0.05$) and the ones in the less benign environment in Shitiangang were larger than the ones measured in the more benign Dexing (paired *t*-test, $P < 0.001$).

Relationships of heritability with plant characteristics

Heritabilities differed significantly among species (ANOVA, $P < 0.001$). The heritability of seed size was not related to any of the five traits, i.e. three species traits (reproductive age, wood density and specific leaf area) and two species distribution measures (range size and marginality). However, across all 13 multiple regressions of the 13 measures of heritability with the five traits, 3 regression coefficients were significant at the $P < 0.01$ level and another 5 at the $P < 0.05$ level (Table 3). In other words, more of the 65 regression coefficients were significant than expected by chance, suggesting that these species and population traits indeed affect heritability.

In the 13 regressions of heritabilities on traits, reproductive age remained in four models, was positively related to the respective heritability for all four, and significantly so for three (Table 3). Wood density remained in seven models, and was positively related to heritability in five cases, and significantly positive for one case. Specific leaf area remained in four models, was positively related to heritabilities in all four cases, and significantly so in two. Thus, species traits were more often related to heritabilities than expected by chance. However, as high reproductive age and wood density are common among K-strategy species, while high specific leaf area is among r-strategy species, there was no clear pattern relating higher heritability to these life-history strategies.

Climatic marginality remained in 3 of the 13 models, each time with non-significantly positive regression coefficients. Moreover, range size remained in eight models, with six positive and two negative coefficients, where the two significant regression coefficients were positive (Table 3).

Overall, our results indicate considerable heritability of seed and plant size for all studied species and suggest that heritabilities are higher for species with larger distribution ranges, higher wood density, higher reproductive age and higher specific leaf area.

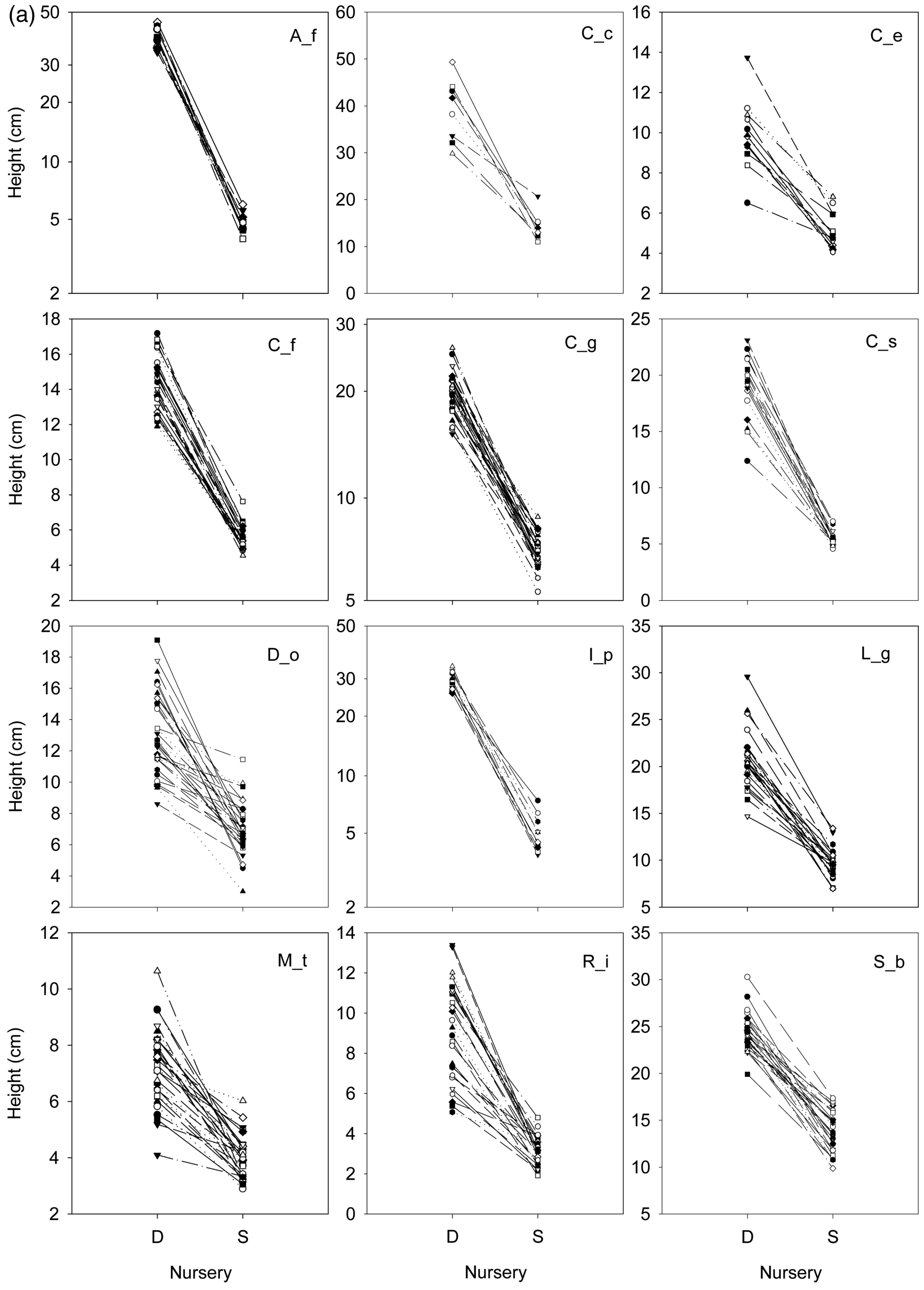

Figure 1: Height (**a**) and basal diameter (**b**) of plants of seed families of 12 subtropical tree species after 7 months of growth in two nurseries with different environmental conditions. See Table 1 for full species names.

DISCUSSION

Heritability of plant performance and phenotypic plasticity therein

Growing replicate seed families of 12–14 tree species in nursery environments clearly revealed considerable and highly significant heritability of seed and plant size among our study species from subtropical China. The heritability estimates suggest considerable potential for evolution of early growth traits, in a life-history phase very important for future community assembly. While there is considerable heritability information for herbaceous plants (Fischer *et al.* 2004; Fornoni *et al.* 2003; Kelly 1993) and commercially important trees (Dvorak *et al.* 2007; Perfectti and Camacho 1999; Stevens and Lindroth 2005), little is known on genetic variation for woody species of natural subtropical and tropical forest (Hahn *et al.* 2017a, 2017b; Li *et al.* 2017a;

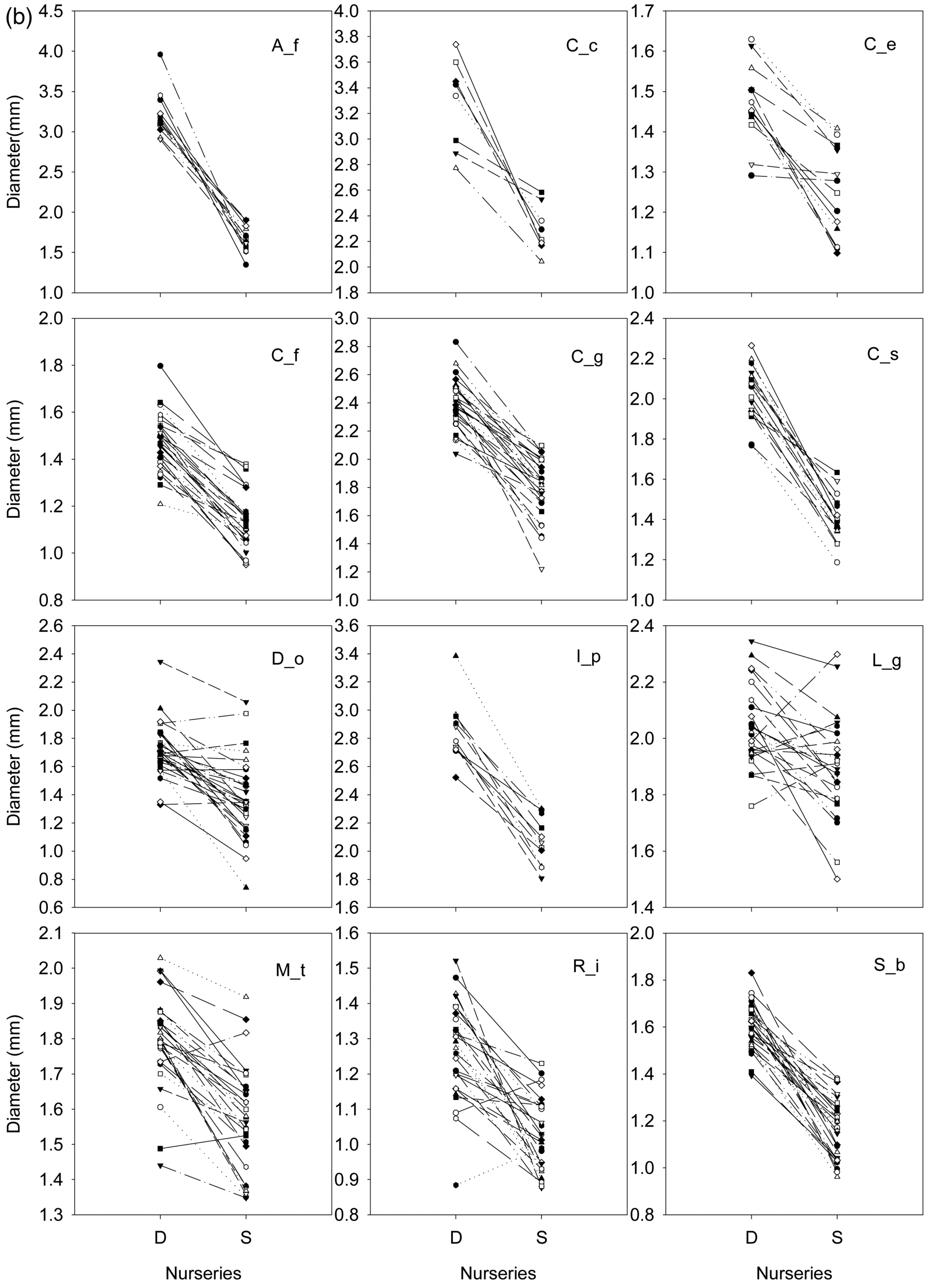

Figure 1: *Continued*

Zeng *et al.* 2017). Our study on woody species of natural subtropical forest suggests that heritability levels in populations of wild subtropical tree species are comparable to the ones of herbs and commercial trees. This considerable heritability suggests that subtropical trees may be able to adapt to changing environmental conditions such as the ones brought about by current global change (Billington and Pelham 1991; Blows and Hoffmann 2005; Jump and Penuelas 2005; Savolainen *et al.* 2004).

The different responses of different seed families to the different nursery environments indicated heritability of phenotypic plasticity in early growth in response to more or less benign conditions (Bradshaw 1965; Pemac and Tucic 1998; Scheiner 1993; Schlichting 1986; Stearns 1992). This suggests that there is not only considerable potential for evolution of early growth traits but also for the evolution of phenotypic plasticity therein. The observed plasticity of higher saplings with wider stems in more benign conditions does not allow us to distinguish in how far this plasticity is rather passive, i.e. driven only by environmental constraints, or rather active, i.e. an adaptive plant response to optimize fitness (sensu van Kleunen and

Table 2: Estimates of heritability h^2 of seed size (subscript *ss*), height (subscript *h*) and diameter (subscript *d*) in the two nurseries Dexing and Shitiangang (subscripts *D*, *S*) for 14 tree species of subtropical China (see Methods)

	Seed size	Height						Diameter					
Species	$h^2_{1\_ss}$	$h^2_{2\_h\_D}$	$h^2_{2\_h\_S}$	$h^2_{2\_h\_mean}$	$h^2_{3\_h\_DS}$	$h^2_{4\_h\_DS}$	$h^2_{h\_all}$	$h^2_{2\_d\_D}$	$h^2_{2\_d\_S}$	$h^2_{2\_d\_mean}$	$h^2_{3\_d\_DS}$	$h^2_{4\_d\_DS}$	$h^2_{d\_all}$
Ardisia crenata		0		0			0	0.18		0.18			0.18
Alniphyllum fortunei		0	0.2	0.06	0.36	0.33	0.14	0	0.34	0.14	0.07	0.13	0.13
Cinnamomum camphora		0.38	0.57	0.47	0.44	0.63	0.47	0.14	0	0.04	0.08	0.27	0.05
Castanopsis eyrei	1	0.09	0.39	0.24	0.22	0.12	0.24	0	0.17	0.08	0.14	0.08	0.09
Castanopsis fargesii	1	0.09	0.23	0.16	0.16	0.07	0.16	0.09	0.14	0.11	0.18	0.07	0.13
Cyclobalanopsis glauca	1	0.18	0.19	0.18	0.23	0.19	0.2	0	0.3	0.15	0.34	0.2	0.2
Castanopsis sclerophylla		0	0.24	0.09	0.31	0.25	0.15	0.05	0.33	0.19	0.12	0.08	0.17
Daphniphyllum oldhamii	1	0.17	0.35	0.26	0.43	0.52	0.3	0.07	0.34	0.21	0.3	0.26	0.23
Eurya muricata	1	0.1		0.1			0.1	0.14		0.14			0.14
Idesia polycarpa	0.57	0.05	0.5	0.28	0.29	0.26	0.28	0.2	0	0	0.25	0.15	0.07
Lithocarpus glaber	1	0.14	0.57	0.35	0.34	0.2	0.35	0.12	0.4	0.26	0.26	0.15	0.26
Machilus thunbergii					0.77	0.57	0.77				0.36	0.06	0.36
Rhaphiolepis indica	0.83	0.23	0.15	0.19	0.27	0.15	0.21	0.05	0.13	0.09	0.11	0.13	0.1
Syzygium buxifolium	1	0.07	0.03	0.05	0.29	0.2	0.11	0.06	0.02	0.04	0.21	0.16	0.08

Heritability estimates >1 were set to 1. Heritability estimates with negative variance-component estimates for differences between seed families were set to 0. The significance of variance components (of seed family for h^2_1, h^2_2 and h^2_3 and of the environment × seed family interaction for h^2_4) was $P < 0.001$, except for the following few cases. $h^2_{3\_d\_D1S1}$: $P = 0.068$ and $h^2_{3\_d\_D1S2}$: $P = 0.028$ for Cc, $h^2_{4\_h\_D2S1}$: $P = 0.022$ for Ip, $h^2_{4\_d\_D1S1}$: $P = 0.314$ and $h^2_{4\_d\_D2S2}$: $P = 0.072$ for Mt, $h^2_{4\_d\_D2S2}$: $P = 0.567$ for Ce (where D1, D2, S1 and S2 denote the blocks in the two nurseries). As h^2_3 and h^2_4 were calculated from four nursery-block combinations, here the block number is additionally indicated after the nursery subscript for the few cases with $P > 0.001$. As *Machilus thunbergii* was sown in one block in each nursery, we give h^2_3 as measure of mean trait heritability and h^2_4 as measure of plasticity.

Table 3: Multiple regression analysis between 13 heritability measures and 5 traits for 14 tree species of subtropical China (see Methods)

	Seed size	Height						Diameter					
	$h^2_{1\_ss}$	$h^2_{2\_h\_D}$	$h^2_{2\_h\_S}$	$h^2_{2\_h\_mean}$	$h^2_{3\_h\_DS}$	$h^2_{4\_h\_DS}$	$h^2_{h\_all}$	$h^2_{2\_d\_D}$	$h^2_{2\_d\_S}$	$h^2_{2\_d\_mean}$	$h^2_{3\_d\_DS}$	$h^2_{4\_d\_DS}$	$h^2_{d\_all}$
Reproductive age									0.04**	0.02*	0.01^+		0.01**
Wood density	2.43		-0.868^+			−0.56			0.62	0.35	0.34		0.33*
SLA					0.02				0.07*	0.03^+			0.02*
Marginality								0.45^+			0.43		0.27^+
Range size		3.54×10^{-4}*		0.1^+		3.89×10^{-4}	$3.07\times10^{-4+}$		$-3.83\times10^{-4+}$	-1.75×10^{-5}	1.85×10^{-4}	2.53×10^{-4}**	
R^2 for the model	0.23	0.40*	0.33^+	0.28	0.24	0.39	0.31+	0.34^+	0.75*	0.66	0.61	0.54*	0.77*

Regression coefficients are given in the table.
$**P < 0.01$, $*P < 0.5$, $^+P < 0.1$.

Fischer 2005). However, the likely fitness relevance of these growth traits in combination with the observed heritable variation in their plasticity suggests that the observed plasticity is active rather than passive (Chi *et al.* 2017; Li *et al.* 2017b).

While maternal carry-over effects may have contributed to heritability estimates especially of seed size, there is little reason to believe that the heritability estimates of plasticity were affected by maternal carry-over effects. Also, such effects are expected to diminish at life-history stages later than seed size (Roach and Wulff 1987; Schmid and Dolt 1994; Vange *et al.* 2004).

Differences between environments

Heritability estimates were larger for the less benign environment than for the more benign one. As heritability estimates measure the proportion of genetically determined phenotypic variation relative to total phenotypic variation, i.e. relative to the sum of genetic and environmental within-treatment variation, this reflects relatively lower environmental variation between replicate plants within seed families in the more stressful environment. This may suggest that the nursery environment in Shitiangang was rather equally stressful for the plants grown there, while the one in Dexing was rather less equally benign for the plants grown there.

Overall, our findings suggest considerable potential for evolution in early growth traits of subtropical trees under benign conditions and even more so under more adverse conditions. Moreover, as mentioned above, high heritabilities of plasticity between nurseries suggest high potential for evolution also for the plasticity of trees of subtropical forest.

Differences between species

We hypothesized that differences among species in their life histories may lead to differences in heritabilities. In particular, we suggested that subtropical tree species with traits more typical for climax species, i.e. trees with higher age at reproduction, denser wood or lower specific leaf area should have higher heritabilities. Multiple regression analysis suggested that heritabilities are indeed higher for species with traits rather indicating K-strategies, i.e. for species with higher age at reproduction and larger wood density. This is in line with the idea that K-strategists rather have high genetic variation within populations (Hamrick and Godt 1996) and suggests that such populations will be especially able to adapt to changing conditions. However, higher heritabilities were also detected for species with higher specific leaf area, i.e. with trait values usually rather associated with an r-strategy, which speaks against our hypothesis. While sampling several populations per species from different regions would add to the generality of our study, there is no reason why our comparisons between heritabilities in species of different strategies should have been biased by the selection of our sampling location. Possibly, the results on specific leaf area are due to the presence of deciduous and evergreen species among our study species, as it is typical for subtropical forest (Lou & Jin 2000), where both deciduous and evergreen tree species occur in different successional stages (Bruelheide *et al.* 2011; Li *et al.* 2017a).

We hypothesized that populations of species with larger distribution ranges may have higher genetic variation. Indeed, several heritability measures were larger for species with larger range size. Moreover, we hypothesized that populations closer to the centre of distribution may have higher genetic variation than populations at the margin (Dlugosch and Parker 2008; Mao and Wang 2011; van Kleunen and Fischer 2008). However, we did not detect significant relationships between heritabilities and marginality. As our study was based on samples of several species from one study region, it will be interesting to see in further studies whether our results on range size are confirmed and whether marginality turns out to matter for heritability when plant origins across the whole range of the study species are considered.

In conclusion, the detected large heritability estimates suggest considerable potential for the evolution of plant performance and its plasticity for trees of subtropical forest. Moreover, they indicate that the simple method of comparing plants of different maternal seed families is valuable to address evolutionary ecological questions for so far understudied species.

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