

A comparative study of growth and leaf trait variation in twenty *Cornus wilsoniana* W. families in southeastern China

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To investigate the genotypic differences associated with the growth potential and leaf traits of *Cornus wilsoniana* W., we planted twenty *C. wilsoniana* families in southeastern China and analyzed nineteen leaf morphological and physiological traits that have potential relationships with growth. Seedling growth and leaf traits exhibited high variability among the *C. wilsoniana* families. The phenotypic coefficients of variation (CVs) of these traits varied from 5.33% (leaf length/leaf width, LL/LW) to 23.17% (stomatal conductance, g_s), and their heritabilities (H^2) ranged from 0.17 (chlorophyll a/chlorophyll b, Chl_a/Chl_b) to 0.75 (stem height, H and Chl_a). There was greater genetic variation in the physiological traits than in the morphological traits. H was significantly positively correlated with instantaneous water use efficiency (WUE), Chl_a , Chl_b and total Chl, and diameter (D) was significantly positively correlated with net photosynthetic rate (P_n), g_s , WUE, Chl_a , Chl_b and total Chl and was negatively correlated with leaf phosphorus (LP). Based on cluster analysis, three families were selected as superior families for the study area due to their seedling growth and leaf traits. These results indicate that P_n , Chl_a , Chl_b and total Chl are good indicators to use for selecting superior families of *C. wilsoniana* with better growth performance; additionally, high WUE and low LP are also critical leaf traits for cultivar selection because plant adaptation to environmental conditions is important for growth performance.

Keywords: Plant Growth, Leaf Traits, Intraspecific Variation, Genetic Heritability

Introduction

Cornus wilsoniana Wangerin is a deciduous tree that is native to South and West China. *C. wilsoniana* is not only a high-quality wood tree but also a biofuel tree with high yield and high oil content (the fruits contain 33-36% oil – Shao & Chu 2008, Li et al. 2010, He et al. 2013). Recently, this multifunctional tree species has rapidly developed in South China, and its area will increase to 2 million hectares by 2020 (Li et al. 2015).

Cultivar selection is an effective method for increasing wood and fruit yield. Genetic

diversity is the foundation of plant breeding. Previous studies have shown that intraspecific variation is lower than interspecific variability (Jung et al. 2010, Kamiyama et al. 2014). In fact, traditional community ecology has mainly focused on interspecific variation, and little work has involved intraspecific variation (Weiher et al. 2011, Violle et al. 2012). However, many studies have shown that there is high variability at the intraspecific level (Ponton et al. 2001, Hulshof & Swenson 2010), provenance level (O'Brien et al. 2007, Rawat & Bakshi 2011) and at the family or clone level (Marron et

al. 2005, Zhao et al. 2016).

Variation in leaf traits is an important component of plant phenotypic plasticity, and it is determined by genetics and the environment (Dudley & Schmitt 1995, Desvignes et al. 2003, Wang et al. 2015). Leaves are the main organs for photosynthesis and are tightly linked to plant biomass production; they are the main exchange platform for water, energy and carbon between the plant and the atmosphere. Leaf traits can reflect plant survival strategies to address environmental changes, and they also reflect plant adaptation strategies to maximize the harvest of carbon. Therefore, understanding variation in leaf traits not only has importance in ecological and biological evolution but also has great significance for plant growth and production. Some leaf traits are good indicators to use in selecting tree species with good growth performance and high biomass productivity (Bunn et al. 2004). Among various leaf traits, leaf area, gas exchange, and intrinsic water use efficiency have been shown to be critical variables in determining plant biomass productivity (Marron et al. 2007, Dillen et al. 2010, Guha & Reddy 2013). Other leaf traits, such as leaf nitrogen concentration and specific leaf area, are sometimes correlated with plant biomass and productivity, which are influenced by tree species, tree age, and growth conditions (Monclus et al. 2005).

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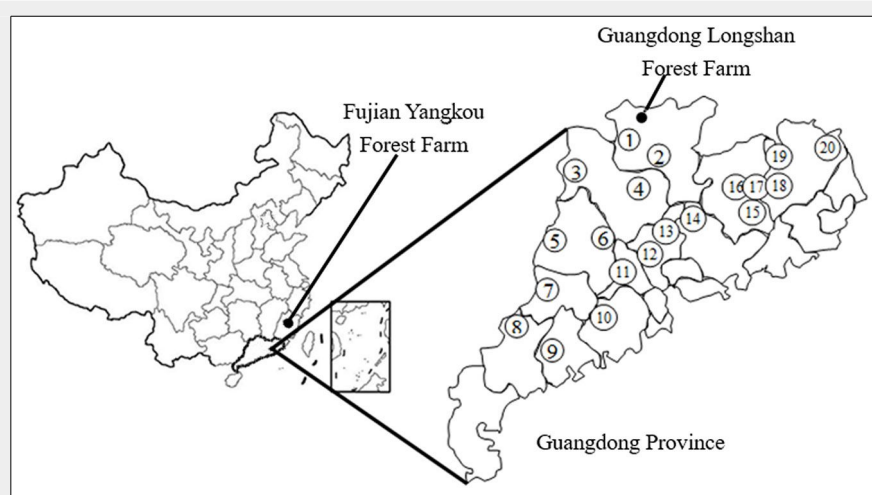


Fig. 1 - Map of China showing the location of the experimental area (Fujian Yangkou Forest Farm), Guangdong Longshan Forest Farm and the plus trees selected in Guangdong Province; numbers inside the circles represent the twenty families.

However, the majority of these results were obtained from fast-growing trees, such as poplar and willow, and some studies were conducted in greenhouses with sufficient water and nutrient supplies. The stability of the relationships between intraspecific variation and leaf traits must be tested using much wider ranges of tree species and environmental conditions.

Although *C. wilsoniana* has recently received more attention and is well documented in silviculture and oil analysis, cultivar selection and the relationship between growth and leaf trait variation in cultivars are less well studied. The objectives of this study were to (1) compare the variation in growth and leaf traits among twenty *C. wilsoniana* families, (2) determine whether leaf traits can predict seedling growth performance, and (3) select superior families for the study area.

Materials and methods

Site description

The study was conducted at the Yangkou Forest Farm (117° 55' E, 26° 47' N, mean altitude 282 m), located in the north of Fujian Province, China. The average annual temperature in the study area is 18.5 °C, the average annual precipitation is 1880 mm, and the frost-free period is 280 days. The study area has a subtropical marine monsoon climate. The average slope is 15% in the experimental area. The soil texture in the study area is clay loam, and the pH is 4.5-4.8. The average contents of soil organic matter, soil available nitrogen and soil available phosphorus are 22.53 g kg⁻¹, 172.71 mg kg⁻¹, and 1.66 mg kg⁻¹, respectively.

Experimental design

The experiment was performed in March 2013 using a randomized block design and included three blocks. Twenty *C. wilsoniana* families were randomly planted in the sub-plots of each block using 2 × 3 m spacing, and there were approximately 100 2-year-old seedlings in each family. The seedlings of the twenty families came from twenty plus trees in Guangdong Province. The seeds of these plus trees were collected and sown in the nursery of Guangdong Longshan Forest Farm. The sites of the selected plus trees, Longshan Forest Farm, and the experimental area are marked on the map in Fig. 1.

Seedling growth and leaf trait measurements

The stem height and ground diameter (5 cm above the ground) of each seedling were measured from July through August 2014. Nine seedlings in the center of each subplot (each family) were randomly selected for sampling. Over 50 mature leaves were collected from these seedlings, which were used to measure leaf length, leaf width and leaf area using the WinFOLIA® Analysis System (Regent Instruments Inc., Canada). The sampled leaves were dried at 75 °C until they reached a constant mass, and then, the dried leaves were ground and passed through a 2 mm sieve. The specific leaf area was calculated using the individual leaf area and dry mass. The total nitrogen and phosphorus concentrations in the leaves were determined using the Kjeldahl method and spectrophotometry, respectively. The leaf nitrogen and phosphorus concentrations are expressed on a dry mass basis.

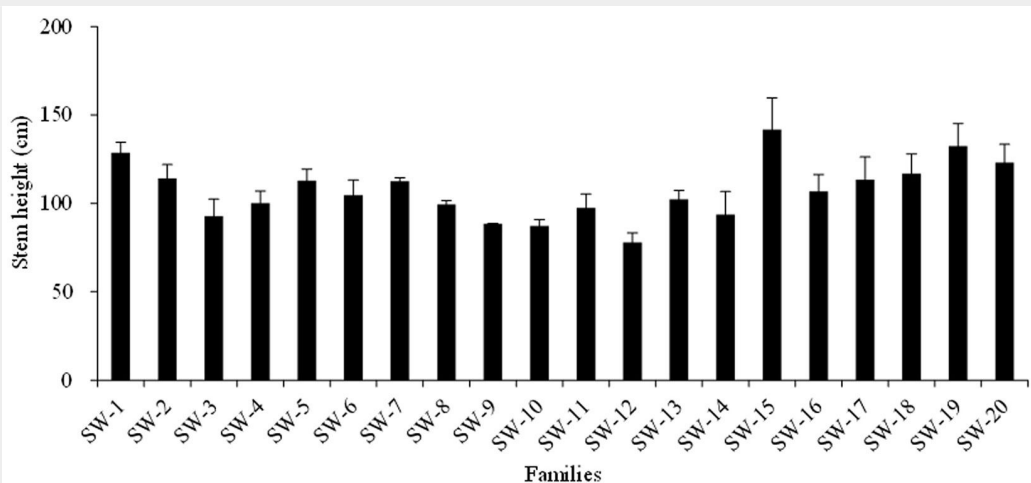
The photosynthetic gas exchange of the leaves was measured with an LI-6400® portable photosynthesis system (Li-Cor, Inc., Lincoln, NE, USA). Six seedlings in each family were selected for the measurement of photosynthetic gas exchange. Four to five fully expanded and exposed leaves from each seedling were selected for the measurement of photosynthetic gas exchange. The photosynthetically active radiation was set to 1000 μmol m⁻² s⁻¹, and light was provided by the red/blue LED light source of the Li-6400. The measurements were carried out from 8:30 to 12:00 p.m. on sunny days. The gas parameters, such as net photosynthetic rate, stomatal conductance, intercellular CO₂ concentration, transpiration rate and instantaneous water use efficiency (WUE), are expressed as average values.

Fresh leaf samples were washed thoroughly with distilled water in the laboratory, dried at room temperature (32 °C) and analyzed for the determination of chlorophyll *a*, chlorophyll *b* and total carotenoid concentrations. The chlorophyll *a*, chlorophyll *b* and total carotenoids in the leaves were extracted using acetone ethanol and then analyzed using a spectrophotometer (723N Jingke, China). See Tab. 1 for the

Tab. 1 - Traits measured in the study.

Variable	Unit	Description
H	cm	Stem height
D	cm	Diameter at 5 cm above the ground
P _n	μmol m ⁻² s ⁻¹	Net photosynthetic rate
g _s	mol m ⁻² s ⁻¹	Stomatal conductance
C _i	mmol mol ⁻¹	Intercellular CO ₂ concentration
T _r	mmol m ⁻² s ⁻¹	Transpiration rate
WUE	μmol mmol ⁻¹	Instantaneous water use efficiency
Chl _a	mg g ⁻¹	Chlorophyll <i>a</i> concentration
Chl _b	mg g ⁻¹	Chlorophyll <i>b</i> concentration
Chl	mg g ⁻¹	Total chlorophyll concentration
Chl _a /Chl _b	-	Chlorophyll <i>a</i> to chlorophyll <i>b</i> ratio
Car	mg g ⁻¹	Carotenoid concentration
Chl/Car	-	Chlorophyll to carotenoid ratio
LL	cm	Leaf length
LW	cm	Leaf width
LL/LW	-	Leaf length to width ratio
LA	cm ²	Average individual leaf area
SLA	cm ² g ⁻¹	Average specific leaf area
LN	mg g ⁻¹	Leaf nitrogen concentration on a dry mass basis
LP	mg g ⁻¹	Leaf phosphorus concentration on a dry mass basis
LN/LP	-	Leaf nitrogen to phosphorus ratio

Fig. 2 - Mean \pm standard deviation (error bars) of the seedling heights of the twenty families.



abbreviations and units associated with these traits.

Data analysis

One-way analysis of variance (ANOVA) was used to test for differences in seedling growth and in leaf physiological and morphological traits among the different *C. wilsoniana* families. The broad-sense heritability (H^2) of each parameter was estimated based on a one-way ANOVA model as $H^2 = \sigma^2_G / (\sigma^2_G + \sigma^2_R)$, where σ^2_G and σ^2_R are the genetic variance and residual variance, respectively (Singh et al. 1993). The correlations between the leaf traits were analyzed by Pearson's correlations with a two-tailed test. Principal component analysis (PCA) was used to summarize the variability in the leaf traits. The traits were standardized, and orthogonal factors (*i.e.*, the PC axes) were established as linear combinations of these traits to distinguish certain key traits. The relationships between seedling growth (such as stem height and diameter) and leaf traits were analyzed using ordinary least squares (OLS) linear regression. To select special functional types among the families, cluster analysis was performed on the seedling growth and leaf traits matrix using Euclidean distances and Ward's linkage method. The number of

clusters was determined by the visual assessment of cluster separation in the dendrogram and in the PCA ordination space. All data analysis was performed using SPSS® 17.0 (IBM SPSS Inc., NY, USA), and the significance level was set at $P < 0.05$.

Results

Plant growth

Stem height (H) and diameter (D) were significantly different among the twenty families ($P < 0.05$). The average H was 107.3 cm; the maximum was 141.8 cm, and the minimum was 77.9 cm. The phenotypic coefficient of variance (CV) was 15.1%. The average D was 1.67 cm; the maximum was 2.10 cm, and the minimum was 1.29 cm. The CV was 13.7%. The H^2 values were 0.75 and 0.73 for H and D, respectively (Fig. 2 and Fig. 3).

Leaf traits

The majority of the leaf traits showed significant differences among the twenty families ($P < 0.05$), but no significant differences were observed for the ratio chlorophyll a/chlorophyll b (Chl_a/Chl_b , $P > 0.05$ – Tab. 2). The CVs were greater than 20% for g_s and C_i ; the CVs varied from 10% to 20% for the

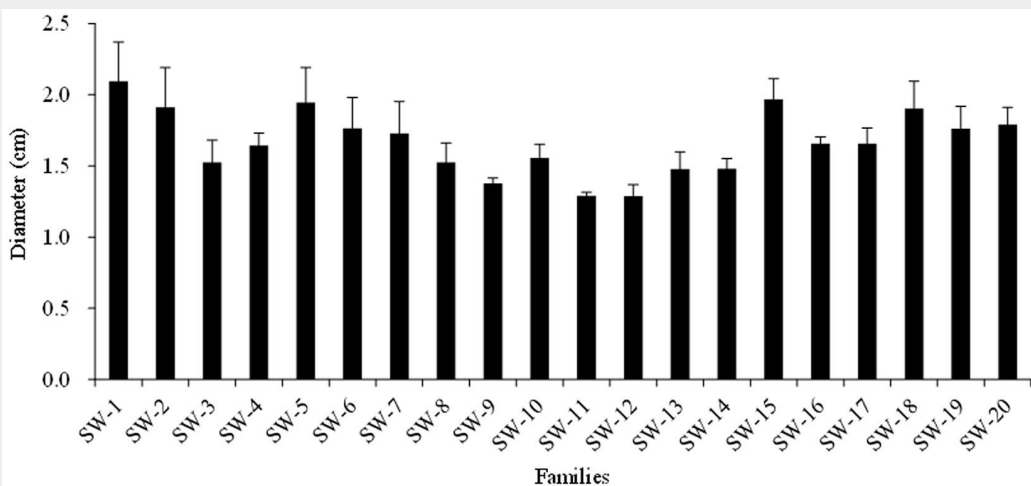
net photosynthetic rate (P_n), transpiration rate (T_r), WUE, Chl_a , Chl_b , Chl, carotenoid concentration (Car), Chl/Car, leaf area (LA), leaf nitrogen (LN) and leaf phosphorus (LP); and the CVs were less than 10% for the other variables. The H^2 was higher for P_n , WUE, Chl_a , Chl_b , Chl, and LN, and it was lower for the other leaf traits, especially for Chl_a/Chl_b (0.17) and Chl/Car (0.31).

Correlations between leaf traits

Pearson's correlation coefficients were determined for all pairwise combinations of leaf traits (Tab. S1 in Supplementary material). The gas exchange variables (P_n , g_s and WUE) were positively correlated with Chl_a , Chl_b and Chl, but only P_n was positively correlated with SLA and negatively correlated with LA. Chl was positively correlated with LN and LP, and Car was positively correlated with SLA and LP. SLA showed a positive correlation with LP and was negatively correlated with LN/LP. There was a positive correlation between LN and LP.

PCA showed that the top 3 principal components explained more than 64% of the total variance (Fig. 4). The first principal component (PC1) accounted for 33.9% of the total variance, which was mainly associated with changes in Chl_a , Chl_b , Chl and P_n .

Fig. 3 - Mean \pm standard deviation (error bars) of the seedling diameters of the twenty families.



Tab. 2 - Descriptive statistics of the leaf traits of twenty families.

Variable	Min	Average	Max	SD	H ²	CV (%)	P
P _n (μmol m ⁻² s ⁻¹)	5.90	8.41	10.52	1.52	0.70	18.04	<0.01
g _s (mol m ⁻² s ⁻¹)	0.044	0.073	0.102	0.017	0.56	23.17	<0.01
C _i (mmol mol ⁻¹)	93.36	141.97	207.92	30.74	0.54	21.65	<0.01
T _r (mmol m ⁻² s ⁻¹)	0.91	1.29	1.62	0.18	0.47	13.62	<0.01
WUE (μmol mmol ⁻¹)	5.21	6.58	8.40	0.80	0.70	12.17	<0.01
Chl _a (mg g ⁻¹)	1.38	1.93	2.57	0.34	0.75	17.78	<0.01
Chl _b (mg g ⁻¹)	0.51	0.77	1.04	0.15	0.64	19.93	<0.01
Chl (mg g ⁻¹)	1.89	2.71	3.59	0.49	0.74	17.97	<0.01
Chl _a /Chl _b	2.18	2.52	3.10	0.24	0.17	9.67	0.12
Car (mg g ⁻¹)	0.69	0.99	1.39	0.18	0.44	17.85	<0.01
Chl/Car	1.78	2.79	3.37	0.49	0.31	17.70	0.02
LL (cm)	8.53	9.81	11.11	0.75	0.54	7.69	<0.01
LW (cm)	3.53	4.27	4.97	0.41	0.48	9.65	<0.01
LL/LW	2.11	2.34	2.58	0.12	0.49	5.33	<0.01
LA (cm ²)	18.32	25.76	33.07	4.23	0.50	16.43	<0.01
SLA (cm ² g ⁻¹)	77.73	89.79	105.29	7.34	0.58	8.18	<0.01
LN (mg g ⁻¹)	11.75	14.62	17.09	1.52	0.71	10.44	<0.01
LP (mg g ⁻¹)	0.75	0.93	1.18	0.12	0.61	13.27	<0.01
LN/LP	13.44	15.82	18.03	1.26	0.48	7.99	0.01

The second principal component (PC2) accounted for 16.6% of the total variance and represented the variation in LP and SLA. The third principal component (PC3) accounted for an additional 13.9% of the total variance, and LA exhibited the highest loading.

The linear least squares regression showed that WUE, Chl_a, Chl_b and Chl were significantly positively correlated with H. The other leaf traits showed no significant linear relationships with H (Tab. 3). D was significantly positively correlated with P_n, g_s, WUE, Chl_a, Chl_b, Chl, LL and LL/LW and negatively correlated with LP but showed no significant correlation with the other leaf traits (Tab. 3).

Cluster analysis

Based on a cluster analysis of leaf traits and seedling growth, the families were classified into four groups (Fig. 5). The first group consisted of SW-6, SW-15, SW-16, SW-17, SW-18 and SW-19; the second group consisted of SW-1, SW-2 and SW-4; the third

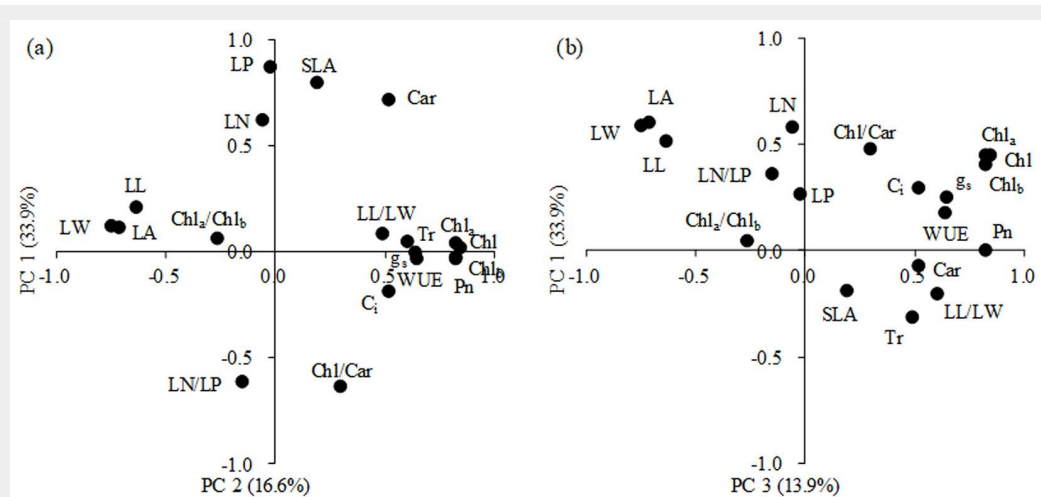


Fig. 4 - Results of the principal component analysis (PCA) of the leaf traits, PC1 against PC2 (a) and PC1 against PC3 (b). The percentages in brackets represent the percent of total variance.

Tab. 3 - Ordinary least squares regression results for the nineteen bivariate relationships.

X variable	Y variable = H				Y variable = D				
	Slope	Intercept	R ²	P	X variable	Slope	Intercept	R ²	P
P _n	4.581	68.772	0.183	0.060	P _n	0.103	0.801	0.469	0.001
g _s	348.170	207.903	0.135	0.111	g _s	6.278	1.213	0.222	0.036
C _i	0.087	94.967	0.027	0.488	C _i	0.002	1.419	0.056	0.315
T _r	1.179	105.790	0.001	0.958	T _r	0.456	1.080	0.122	0.131
WUE	11.166	33.869	0.302	0.012	WUE	0.169	0.558	0.349	0.006
Chl _a	29.635	50.024	0.393	0.003	Chl _a	0.410	0.876	0.380	0.004
Chl _b	51.516	67.436	0.239	0.029	Chl _b	0.766	1.075	0.267	0.020
Chl	19.957	53.286	0.357	0.005	Chl	0.281	0.906	0.360	0.005
Chl _a /Chl _b	12.088	76.860	0.033	0.442	Chl _a /Chl _b	0.051	1.539	0.003	0.818
Car	17.106	90.425	0.034	0.433	Car	0.314	1.358	0.059	0.302
Chl/Car	11.203	76.068	0.115	0.143	Chl/Car	0.141	1.275	0.092	0.193
LL	-0.613	113.322	0.001	0.905	LL	-0.092	2.575	0.094	0.190
LW	-8.978	145.692	0.052	0.335	LW	-0.282	2.871	0.256	0.023
LL/LW	49.944	-9.735	0.145	0.098	LL/LW	0.932	-0.517	0.254	0.024
LA	-0.495	120.066	0.017	0.588	LA	-0.022	2.242	0.170	0.071
SLA	-0.420	144.981	0.036	0.423	SLA	-0.002	1.882	0.006	0.748
LN	-0.357	112.512	0.001	0.887	LN	-0.051	2.410	0.117	0.140
LP	-33.648	138.585	0.065	0.277	LP	-0.852	2.460	0.212	0.041
LN/LP	1.876	77.626	0.021	0.539	LN/LP	0.023	1.299	0.017	0.587

group consisted of SW-7, SW-9, SW-13 and SW-14; and the fourth group consisted of SW-3, SW-5, SW-8, SW-10, SW-11, SW-12 and SW-20. Collectively, the families in the first and second groups exhibited higher performance in most of the studied traits than did those in the third and fourth groups. The three families in the second group performed better than those in group 1 in terms of P_n , WUE, SLA, and diameter growth rate, and the third group exhibited lower performance in P_n and SLA than the fourth group.

Discussion

Variation in growth and leaf traits

It is very important to understand the genetic variation within species, families or clones for plant breeding (Safavi et al. 2010). The CV and H^2 are two key parameters for evaluating the extent of variability in a breeding population and in selecting cultivars (Liu et al. 2015). High phenotypic variability in a species benefits cultivar selection. In the current study, we found that growth and most leaf traits exhibited significant differences and great variation among the twenty families, with the CVs of different traits varying from 5.33% to 23.17%. This finding is in accordance with previous studies (Marron et al. 2005, 2007, Li et al. 2008, Kanaga et al. 2008, Verlinden et al. 2013, Wang et al. 2015). Zhao et al. (2016) showed that the CVs of H and diameter at breast height (DBH) varied from 15.37% to 20.85% for 44 *Betula platyphylla* families. Pliura et al. (2007) reported that the CVs of H and DBH varied from 10.05% to 31.60% among poplar clones at different sites. The CVs of H and D in the present study were lower than those in these previous studies, which may be due to differences in the plant species, the numbers of families or clones or the environment.

High heritability was observed for stem height ($H^2=0.75$), diameter ($H^2=0.73$), P_n ($H^2=0.70$), WUE ($H^2=0.70$), Chl ($H^2=0.64-0.75$) and LN ($H^2=0.71$). This result indicates that these traits showed high diversity among the families and low sensitivity to the microenvironmental heterogeneities in the study area. By contrast, Chl_a/Chl_b ($H^2=0.17$), Chl/Car ($H^2=0.31$) and leaf size (H^2 varied from 0.48 to 0.54) displayed low heritability, which may be due to low inter-family variability.

Plant physiological and morphological plasticity may play different roles in response to environmental changes. Recently, a review by Gratani (2014) indicated that in colonized gaps and open areas, the plasticity of physiological traits plays a dominant role because it ensures adjustments in gas exchange in response to changes in environmental factors. Leaf morphology tends to be maintained under stress conditions to avoid the production of structures too expensive to be sustained (Chapin III et al. 1993, Valladares et al. 2000). Additionally, morphological plastic-

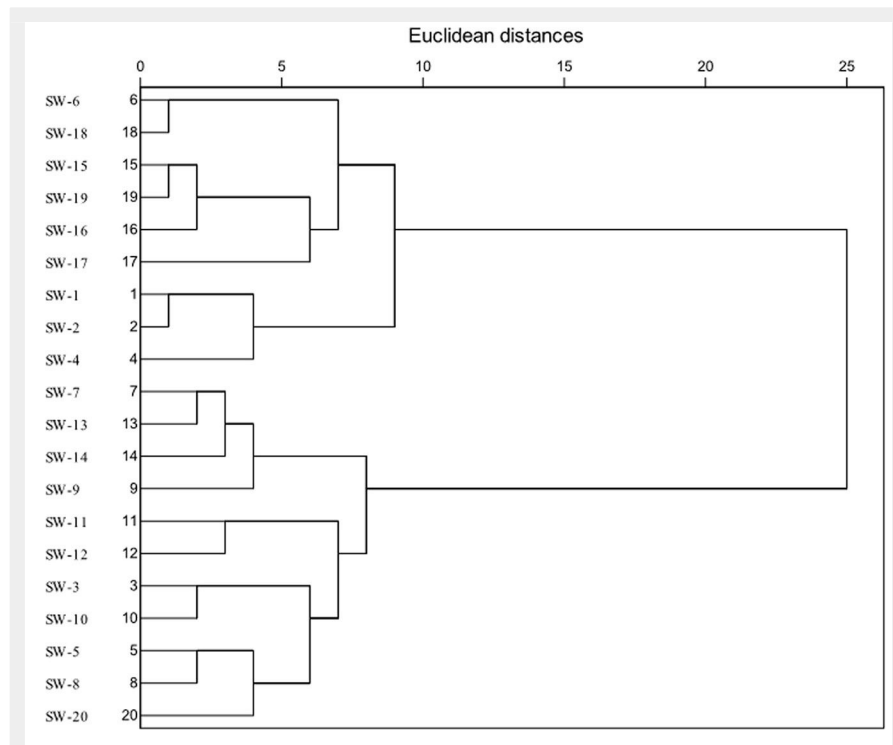


Fig. 5 - Cluster analysis of different families of *C. wilsoniana*.

ity is closely linked to the capacity of a plant to acquire resources in forest understories (Navas & Garnier 2002, Niinemets & Valladares 2004). In this study, the variation in leaf physiological traits was greater than that in morphological traits (Tab. 2). The results from the PCA also confirmed that the proportion of the leaf physiological traits accounting for the total variance was greater than that of the morphological traits (Fig. 4). However, some studies have found that the genetic variation among tree genotypes in terms of morphological traits was greater than that for physiological traits (Müller et al. 2012, 2013). The difference might be explained by two factors. First, the present study was conducted at a single site, which results in less variation in environmental conditions; the physiological traits with high CVs also exhibited greater H^2 , which implies that a difference in tree species might be an important factor that leads to different results. Second, the present study included a smaller number of morphological traits.

The twenty families in this study represent a very small subset of the actual population. Additionally, phenotypic plasticity results from phenotypic variation due to genotype and the environment, as well as their interactions; thus, the levels of phenotypic variation may be higher in natural *C. wilsoniana* stands.

Leaf traits related to growth

The parameters of tree stem growth, such as H and D (or DBH), are often used to evaluate tree growth performance because these two parameters are directly associated with aboveground biomass

(Pellis et al. 2004, Marron et al. 2005, Selaya & Anten 2008). In the present study, H was significantly positively correlated with WUE, Chl_a , Chl_b , and Chl and showed a relatively weak correlation with P_n ($P = 0.060$). D was significantly positively correlated with P_n , g_s , WUE, Chl_a , Chl_b , and Chl and was negatively correlated with LP. P_n is closely associated with biomass and productivity in many plant species; however, it is not always positively correlated with tree growth and biomass, which might be due to photosynthetic complexity, different carbon allocation patterns, or sampling error while collecting photosynthesis data (Dillen et al. 2010, Flood et al. 2011). Reddy et al. (2003) confirmed that Chl_a , Chl_b , the Chl_a/Chl_b ratio and the total Chl showed significant positive correlations with leaf area and yield in different genotypes of mulberry (*Morus* spp. L.). Therefore, our results indicate that families with higher P_n and chlorophyll content have the potential for better growth performance. A higher WUE would be beneficial for seedling survival and growth in arid habitats, where reducing water loss allows a tree to avoid dehydration and extend water use. In recent years, the seasonal drought frequency has increased in the study area. At the same time, the families with low LP may be better adapted to phosphorus-deficient soils.

Leaf area, total leaf area and leaf number per plant have been considered to be good indicators and have been used to predict the productivity of fast-growing poplar and *Salix* species (Yu et al. 2001, Weih 2009). Some studies have shown that H and D are positively correlated with leaf area and

total leaf area (Rae et al. 2004, Marron et al. 2005). In the current study, although D was positively correlated with LW and LL/LW, no significant correlation was observed between D and LA. Therefore, compared to the average leaf area, the total leaf area per plant may be more important for predicting plant growth because a larger total leaf area suggests that the plant can capture more light. However, the present study did not investigate the total leaf area per plant.

Many studies have shown that P_n is significantly correlated with LN or SLA and that LN and SLA play key roles in the photosynthetic process. We found that only P_n was positively correlated with SLA; no significant correlations were observed between the two variables and H and D. Some studies have shown a positive correlation between SLA and relative growth rate (RGR – Poorter & Garnier 1999, Veneklaas et al. 2002). Other studies have reported that SLA was negatively correlated with biomass production (Nelson 1988, Wright et al. 1994, Thumma et al. 2001). These different results for the relationship between SLA or LN and growth or productivity depended on species, growth conditions and tree age (Monclus et al. 2005).

In this context, additional studies are needed to test: (i) whether the ranking of these families in terms of growth performance based on leaf traits remains stable over time; (ii) whether these results can be extended to clones; and (iii) the relationship between leaf traits and fruit yield at the level of families or clones.

Conclusion

This study confirmed that seedling growth and leaf traits display high variability among twenty *C. wilsoniana* families and suggested greater genetic variation in physiological traits than in morphological traits. P_n , WUE, Chl_a , Chl_b , Chl_a/Chl_b , total Chl and LP could be used together to select families with the best growth performance. Plant adaptation to specific environments is a key factor to consider to increase growth and productivity. Based on the variation in seedling growth and leaf traits, 3 superior families were selected for this study area.

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Conflict of Interest

The authors declare that they have no conflicts of interest.

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Supplementary Material

Tab. S1 - Pearson's correlation coefficients between leaf traits.

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