

Genetic variability and heritability of some morphological and physiological traits in *Fagus orientalis* Lipsky along an elevation gradient in Hyrcanian forests

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Abstract

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The purpose of the present study was to evaluate the genetic variability and heritability of some morphological and physiological traits in *Fagus orientalis* Lipsky along an elevation gradient in northern forests of Iran. Beech leaves were sampled from southern and northern crown parts of healthy mature trees along an elevation gradient comprising sites situated at 700 m, 1,200 m and 1,700 m above the sea level. Our statistical analysis showed that the investigated traits differed significantly between the populations. The results indicated the lowest and the highest coefficients of variation for the high (1,700 m) and middle elevation populations (1,200 m) for leaf length, petiole length, leaf area, specific leaf area, dry weight, specific dry weight, leaf index and petiole index traits. With increasing elevation, mean leaf width, distance from leaf base to the leaf maximum width, dry weight and petiole index increased. The plasticity of leaf length, specific leaf area, specific dry weight, petiole index and petiole length peaked at middle elevation, and with increasing elevation, the plasticity of these traits declined. The distance from leaf base to the leaf maximum width had the highest coefficient of genetic (75.5%) and phenotypic (75.5%) variation. The heritability results showed that there were differences in all traits, and that the highest heritability was recorded for the distance from the leaf base to the leaf maximum width (99.95 %). The results suggest that the studied beech populations responded to the environmental changes by changing their leaf traits in different ways at different altitudes.

Keywords

correlation, elevation change, heritability, *Oriental beech*, leaf trait, plasticity

Introduction

Climatic change in recent decades has been recognized as a potential driver causing shifts in plant physiological and phenotypical processes. For improving predictions of species survival and providing accurate conservation planning

under the increasing environmental pressure caused by the climate change, it is necessary to understand the interactions between morphological and physiological traits in plants and these plant response to environmental changes. Changes in the environmental (ecological and edaphic) and climatic conditions such as temperature, rainfall and

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solar radiation can provide an ideal experimental setting for evaluation of the species adaptation (PAULI et al., 2007). Variations in the environmental conditions along elevation gradients lead to selection pressures by climate change. The responses to these selection pressures can be different among the species. Elevation gradients provide a suitable experimental setting for studying changes in plant functional traits in response to environmental changes and the implications of these variations for the populations capacity to respond the changes in their environmental conditions (KÖRNER, 2007). The morphological traits of leaves in tree species can provide a rich information about evolution of genetics and phenotypic diversity. Recently, different markers such as morphological, protein and molecular markers, including RAPD, SSR, RFLP and AFLP are used to survey genetic diversity. The success of a species in response to its natural selection pressures along different environmental gradients in context of climatic changes depends on the inheritance of genetic variation within the species (CLAIR et al., 2010). Plant populations with high genetic diversity can be suitable for genetic conservation. Therefore, to ensure better management and conservation of forests sources, the information about the genetic diversity among the populations is essential (SCOTTI et al., 2010). Quantitative genetic diversity is the basis for interactions between the environments and the natural populations and the evaluation of genetic diversity is crucial for forest management (SCOTTI et al., 2010). Previous studies have shown that along an elevation gradient, leaf morphology can vary noticeably. For example, AKBARIAN et al. (2011) studied the effect of altitude on the whole leaf and stomatal morphology in *Alnus subcordata* in the Hyrcanian forests and found that correlation analyses showed a significant, positive relationship between tooth numbers and altitude. Also, significant divergences among natural populations of *Parrotia persica* were observed along an elevation gradient in the Hyrcanian forests (SATTARIAN et al., 2011). Similarly, variations in leaf macro- and micro-morphological variability in *Carpinus betulus* were observed along an elevation gradient in the Hyrcanian forest (CHAPOLAGH PARIDARI et al., 2013). ZOLFAGHARI et al. (2013) calculated different genetic parameters such as heritability, genetic and phenotypic variation coefficients, and the inter- and intra-populations variance for *Quercus brantii* Lindl. The results of this author showed that leaf area, leaf weight and relative water content had high heritability between the populations.

The present study was carried out to investigate the effect of elevation on some morphological and physiological traits in beech species. The aims of this study were: 1) to determine the quantity and type of variation (phenotype or genotype) in *Fagus orientalis* in Hyrcanian forests of Iran; 2) to investigate the changes in leaf traits along elevation gradients within and between the populations of *Fagus orientalis*; 3) to identify the extent to which these variations are under genetic or phenotypic control, and 4) to estimate the heritability of traits.

Materials and methods

Study area

This study was conducted in the Masal forests of the Guilan province, Iran. Hyrcanian forests are ancient and unique forest communities located in the northern Iran. Beech (*Fagus orientalis* Lipsky) is one of the most important deciduous species in these forests. Hyrcanian forests are found at elevations from 600 to 2,000 m (AHMADI et al., 2009). Pure and mixed beech (*F. orientalis*) forests are the most important elements of this ecosystem, they represent the richest and the most beautiful forests of Iran. Three sampling sites were selected along an altitudinal transect. Sampling was done in natural stands of *F. orientalis* (Alborz mountains, 37°14' and 37°19'20" N, 48°55'19" and 49°02'E, Iran; Fig. 1). Mean annual precipitation and temperature are 926 mm and 21.3 °C, respectively. Mean annual precipitation and temperature in the growing season from April to September are 394 mm and 26.6 °C, respectively (Fig. 2).

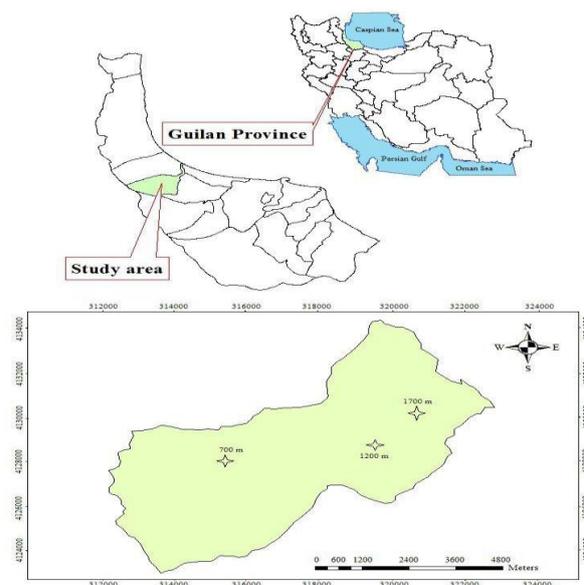


Fig. 1. Location of the study area.

Sampling method

The leaves were sampled on beech trees at low (L; 700 m a.s.l.), middle (M; 1,200 m. a.s.l.) and high (H; 1,700 m a.s.l.) elevations (Table 1). At each elevation, twenty dominant trees with the same size were selected randomly for leaf measurements in August 2016. A global positioning system receiver (GPS) was used to determine the exact elevation for each population. Twenty expanded leaves were collected from each mature and healthy tree. All of the leaf samples were collected from the middle part of the canopy (CHAPOLAGH PARIDARI et al., 2013) (Table 2).

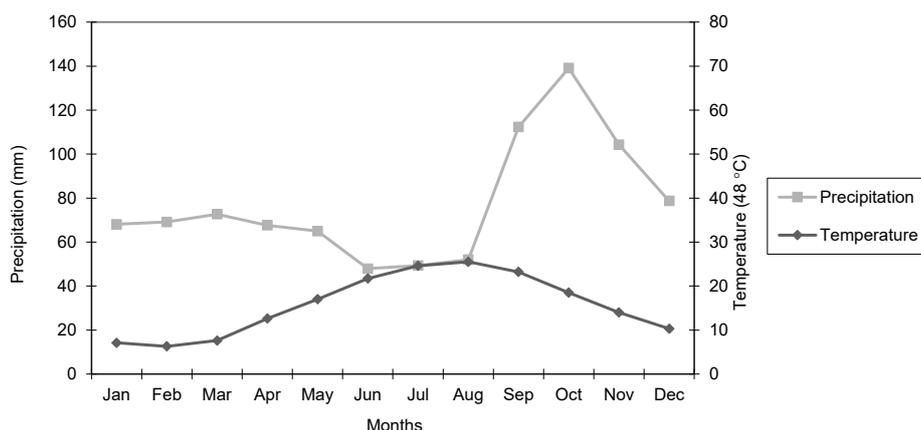


Fig. 2. Climadiagram of the study site.

Table 1. Details of three populations along elevation gradients

Locality	Altitude (m)	Lat. (N)	Lon. (E)	Slope	Aspect	Monthly average* Temperature (°C)
Low	700	37°16'30"	48°54'01"	25–30	North-northeast	25.64
Middle	1,200	37°17'40"	48°57'21"	35–40	Eastern-Southeast	26.47
High	1,700	37°18'16"	48°58'30"	60–65	North-northeast	25.28

*Monthly average temperature in the growing season.

Table 2. Morphological and physiological traits of measured leaves

Abbreviation Leaf	Morphological and physiological traits	Unit
LL	Leaf length	cm
LW	Leaf width	cm
PL	Petiole length	cm
BW	Distance from leaf base to the leaf maximum width	cm
LA	Leaf area	cm ²
DW	Dry weight	gr
SLA	Specific leaf area (leaf area/dry weight)	cm ² /gr
SDW	Specific dry weight (dry weight/leaf area)	gr/cm ²
RWC	Relative water content	%
LI	Leaf index	
PI	Petiole index	

Morphological and physiological analysis

Morphological traits including LA, LL, LW, PL and BW (Table 2) were tested for each leaf with a ImageJ ver. 1.44 software (<https://imagej.nih.gov/ij>). The leaves were dried at 80 °C for 72 hours, and then there were weighed using an electric scale for the calculation of specific leaf area (SLA). The SLA ratio was defined as the ratio between the mass of dried leaves and their leaf area. Leaf index (LI) and petiole index (PI) were calculated according to the following equations $LI = ((LL/LW) \times 100)$ and $PI = ((PL/LL) \times 100)$ (HATZISKAKIS et al., 2011). Relative leaf water content (RWC) was calculated as: $RWC = (FW - DW)/(SW - DW) \times 100$, where FW was the leaf fresh weight, DW the leaf weight after drying at 80 °C for two days, and

SW was the leaf weight after rehydration until saturation for 48 h (SALVADOR, 2004). Furthermore, SW/DW ratio was calculated as the ratio between the saturation and dry weight. Environmental and genetic variance components were estimated based on the expected mean square value. Phenotypic (δ_p^2) and genotypic (δ_g^2) variances were calculated following BAYE (2002):

$$\delta_e^2 = \frac{MS_e}{r} \quad (1)$$

$$\delta_g^2 = \frac{MS_p - MS_e}{r}, \quad (2)$$

where MS_p, MS_g, MS_e were mean squares values of phenotypes, genotypes and error, respectively; r was the replication.

Phenotypic and genotypic coefficients of variation (PCV and GCV) and heritability (h^2) were calculated according to the HALLUER and MIRANDA (1998):

$$PCV = \frac{\sqrt{\delta_p^2}}{\bar{X}} \times 100 \quad (3)$$

$$GCV = \frac{\sqrt{\delta_g^2}}{\bar{X}} \times 100, \quad (4)$$

$$h^2 = \frac{\sigma_g^2}{\sigma_p^2}, \quad (5)$$

where PCV, GCV, h^2 were phenotypic coefficient, genotypic coefficient and heritability respectively, (σ_p^2) and (σ_g^2) were phenotypic variances and genotypic variances.

The phenotypic differentiation coefficient (V_{ST}) was calculated using the following equation:

$$V_{ST} = (o'_{t/s}) / (o'_{t/s} + o'_{t}),$$

where $o'_{t/s}$ is the percentage of variance between populations and o'_{t} is the percentage of variance within populations.

The total within-transect plasticity (PL) was calculated for each parameter using the lowest and highest mean values, using the following equation:

$$PL = 1 - (x/X),$$

where x is the lowest value and X is the highest value for any given leaf trait measured (BRUSCHI et al., 2003).

Statistical analysis

Before the analysis of variance, the data for the individual parameters were tested using the Kolmogorov-Smirnov test for normality. The responses of traits to elevation were analyzed using a General Linear Model (GLM). Then,

using nested variance analysis (Nested ANOVA), inter-population and intra-population changes were investigated. Duncan post-hoc ($P < 0.05$) test was used for the means comparison. These analyses are performed using the following statistical model:

$$Y = \mu + P + T(P) + \varepsilon,$$

where Y is the dependent variable, μ is the overall mean of the analyzed traits, P is the population (evaluation of the environmental variability between different altitudes), T (P) is the interaction between the population and tree (between individual variability – genetic variability), and ε is the total error of the model. A Pearson correlation analysis was performed to identify significant correlations between variables. All statistical analyses were conducted using the SAS 9.0 software (SAS Institute Inc., Cary, NC, USA, 2002).

Results

The analysis of variance performed using nested ANOVA showed that there was a significant difference between three populations for LW and BW traits and also there was a significant difference within populations for LW trait (Table 3). The analysis of variance for morpho-physiological traits showed that there was a significant difference among populations for LA, SLA, SDW and RWC traits (Table 3).

Mean values, coefficients of variation, and standard deviations are listed in Table 3. Leaf traits at the middle elevation had the highest coefficients of variation (CV) for LL, PL, LA, SLA, DW, SDW, LI and PI traits. The lowest CVs belonged to the upper elevation (1,700 m a.s.l.). The mean values increased for LW, BW, DW and PI with increasing elevation and they had significant linear trends along the elevation gradients. The mean values for LA, SLA and RWC increased with elevation at low and middle

Table 3. Results of variance analysis for the measured traits in beech populations

Traits	Source		
	Population	Population × aspect of crown	Error
df	2	3	57
LL	0.184 ^{ns}	9.647 ^{ns}	4.763
LW	29.931*	2.783*	46.943
PL	0.032 ^{ns}	0.01 ^{ns}	0.024
BW	17.467*	0.454 ^{ns}	0.389
LI	0.1439 ^{ns}	0.22082 ^{ns}	0.1523
PI	0.00005 ^{ns}	0.0002 ^{ns}	0.0001
LA	*29135.93	2296.783*	463.943
SLA	*34660.75	1317.76 ^{ns}	4119.820
DW	0.156 ^{ns}	0.022 ^{ns}	0.703
SW/DW	17.467*	0.454 ^{ns}	0.289
SDW	*4.632	0.0 ^{ns}	0.0
RWC	4.608*	0.00 ^{ns}	0.000

elevations but decreased with elevation at high elevation (Table 4). The mean values of LL, PL and SW/DW decreased at the middle elevation but increased at the upper elevation (Table 4). The results of plasticity among the population showed that LL, SLA, SDW, PL and LI increased at the middle elevation but showed decreasing trends with increasing elevation. In addition, mean values for some traits such as LW and LW were decreasing and the value of DW increased with elevation (Table 4, Fig. 3).

Variance components, coefficient of variation and

heritability of leaf traits are shown in Table 5. The results show that the highest coefficients of genotypic variation were obtained for BW, SDW and SW/DW (75.455, 36.38 and 22.17, respectively) which indicates high variability in the measured variables in beech trees. Also, the highest heritability belonged to BW, LA, RWC and SLA (99.95, 98.43, 88.43 and 88.11, respectively) (Table 5). The phenotypic differentiation coefficient (V_{ST}) of the measured traits was 70.72%, which indicates mainly differentiation among the populations.

Table 4. Descriptive statistics for the measured leaves traits

Traits	Elevations	Mean	SD	CV (%)
LL	L(700 m)	11.545	1.848	16.009
	M(1,200 m)	11.412	3.471	30.421
	H(1,700 m)	11.458	1.172	10.231
LW	L(700 m)	5.545a	0.839	15.136
	M(1,200 m)	5.796a	0.841	14.516
	H(1,700 m)	5.856b	0.552	9.437
PL	L(700 m)	0.665	0.188	28.278
	M(1,200 m)	0.629	0.184	29.355
	H(1,700 m)	0.685	0.168	9.793
BW	L(700 m)	5.149a	0.845	16.416
	M(1,200 m)	5.163b	0.549	10.638
	H(1,700 m)	6.300ab	0.617	10.951
LA	L(700 m)	89.770a	22.489	25.051
	M(1,200 m)	139.214b	43.518	31.259
	H(1,700 m)	133.245ab	24.034	18.037
SLA	L(700 m)	272.130a	79.278	29.132
	M(1,200 m)	330.767b	117.841	35.626
	H(1,700 m)	306.014ab	66.231	21.643
DW	L(700 m)	0.3465	0.1009	29.129
	M(1,200 m)	0.449	0.143	32.009
	H(1,700 m)	0.459	0.136	29.753
SW/DW	L(700 m)	5.943	3.746	63.043
	M(1,200 m)	3.362	0.910	27.088
	H(1,700 m)	4.386	6.003	136.857
SDW	L(700 m)	0.004a	0.001	33.072
	M(1,200 m)	0.003b	0.001	39.221
	H(1,700 m)	0.003b	0.0007	22.630
RWC	L(700 m)	28.046a	16.709	59.578
	M(1,200 m)	37.668b	0.9108	35.776
	H(1,700 m)	37.266b	6.003	31.146
LI	L(700 m)	2.082	0.1461	7.019
	M(1,200 m)	2.002	0.719	35.914
	H(1,700 m)	1.965	0.215	24.844
PI	L(700 m)	0.057	0.014	24.392
	M(1,200 m)	0.057	0.0202	35.054
	H(1,700 m)	0.059	0.012	21.647

L, M, and H, respectively, refer to the oriental beech population at 700, 1,200 and 1,700 m a.s.l. For the abbreviations of traits, refer to the Table 2.

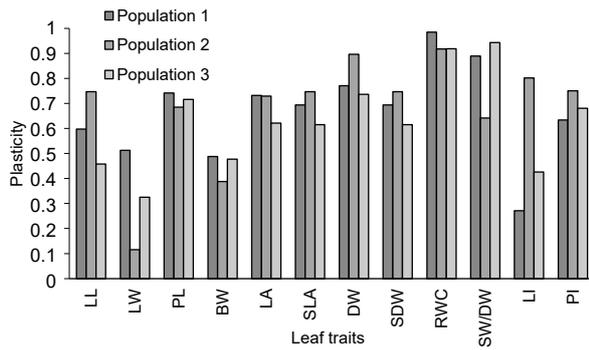


Fig. 3. Results of plasticity (PL) for leaves traits in three populations. Population 1, 2, and 3, respectively, refer to the oriental beech population at 700, 1,200 and 1,700 m a.s.l. For the abbreviations of traits, refer to the Table 2.

The results of correlation coefficient showed that there was a significant and positive correlation between of LL and LW ($r = 0.99$, $P = 0.01$), and between of PL and LA ($r = 0.57$, $P = 0.01$). Also, these results showed that there was a significant and negative correlation between LA and SDW ($r = 0.45$, $P = 0.01$). The results of correlation coefficient are listed in Table 6.

Discussion

Leaves morphological and physiological traits are affected by different conditions along elevation gradients (THOMAS, 2011) and the effects of altitude on leaf morphology and physiology are important for plant development (AKBARIAN et al., 2011). In this study, the results of mean comparison showed that LW, BW, DW and PI increased with increasing elevation among different populations. At higher elevations, trees should be located horizontally – to receive more light, so the petioles are prolonged. This change reflects the adaptation of the *Fagus orientalis* to the environmental conditions in each habitat. Our results are

in line with other findings in various environments, such as variation in LW and BW (CHAPOLAGH PARIDARI et al., 2013). The low values of leaf area in upper elevations may be a beneficial mechanism for coping with some stresses such as high light intensity and drought. In fact, decreasing leaf area is beneficial at high water stress and light intensity stress, as it causes the leaf area to be smaller and reduce the transmission rate (ZAMBRANO et al., 2014). The total solar radiation and ultraviolet radiation increase with increasing elevation. Under high degree of radiation, trees do not expand their leaf area – to prevent light damage. This finding is consistent with the results of GHORBANLI et al. (2013) who studied the effect of altitude on leaf area variation in *Carpinus betulus*, and Royer et al. (2008) in *Acer rubrum*. The SDW values decreased with increasing elevation. The higher SDW is probably a result of higher temperatures and summer drought at lower elevations as well as lower temperature at higher elevations (BRESSON et al., 2011). This result is consistent with the findings reported in previous studies (CHAPOLAGH PARIDARI et al., 2013; GRATANI et al., 2012). Also, this result is consistent with the findings of GUO et al. (2017), which showed an opposite pattern in SDW and RWC values in the shrubs along elevation gradients. POULOS et al. (2012) showed that RWC changed more within elevation gradients for four pine species. The analysis of variance indicated that the variation among populations was higher than variation within populations (Table 3). Similar results were reported by STOJNIC et al. (2016) who studied the intra- and inter-provenance variations in leaf morphometric traits in *Fagus sylvatica* in the northern part of Serbia. In addition, the study of BAYRAMZADEH et al. (2012) on the variations of leaf morphological traits in the natural population of *Fagus orientalis* in the Caspian forests of northern Iran showed the similar results. According to the results, the differences among populations may compromise the effects of climate change (change in temperature, precipitation) occurring along elevation gradients. This result coincides with the results of HATZISKAKIS et al. (2011), and the high phenotypic diversity among populations improves their adaptation to different environmental conditions occurring along

Table 5. Variance components, coefficient of variation and heritability of leaves traits

Traits	Estimated variance components			CV%		V _{st} %	Heritability%
	Phenotype	Genotype	Environment	Phenotype	Genotype		
LL	0.0046	-0.1144	0.119	0.2387	1.1909	3.72	-24.88
LW	0.0271	0.0171	0.0099	1.1471	0.9118	73.087	63.17
PL	0.0008	0.0001	0.0006	5.7093	2.72	56.445	22.83
BW	17.4703	17.4631	0.0072	75.4707	75.455	99.958	99.95
LA	728.3984	716.799	11.5985	22.3521	22.1734	98.432	98.43
SLA	866.5189	763.523	102.9955	9.71602	9.1203	89.376	88.11
DW	0.006	0.00	0.00	20.19	18.93	92.678	87.89
SW/DW	1.6884	1.3512	0.3371	28.5187	25.5127	83.354	80.03
SDW	3.43	2.74	0.68	40.65	36.38	85.803	83.45
RWC	29.6242	26.199	3.4251	15.8252	14.8823	89.636	88.43
LI	0.0035	-0.0002	0.0038	3.0278	0.7313	48.595	-5.78
PI	0.000001	0.000002	0.000003	-0.0203	3.8053	27.581	-61.91

Table 6. Pearson correlation analysis of measured traits in the beech population

	LW	PL	BW	LA	SLA	DW	SD/SW	SDW	RWC	LJ	PI
LL	0.99**	-0.75**	-0.18*	-0.39**	-0.12	-0.27**	0.18*	0.07	-0.25	0.34**	-0.11
LW		-0.74**	-0.19*	0.53**	-0.13	-0.25**	0.18*	0.08	-0.28**	0.34**	-0.10
PL			0.45**	0.57**	-0.01	0.60**	-0.01*	-0.02	0.26**	-0.38**	0.43**
BW				0.35**	0.02	0.34**	-0.07	-0.13	0.10	0.07	0.07
LA					0.43**	0.55**	-0.12	-0.45**	0.04	-0.07	-0.004
SLA						-0.47**	-0.07	-0.91**	-0.18*	0.10	-0.41**
DW							-0.06	0.42**	0.21*	-0.19*	0.35**
SW/DW								0.05	-0.43**	0.05	-0.05
SDW									0.14	0.09	0.35**
RWC										-0.15	0.05
LJ											-0.22*

For the abbreviations of traits, refer to the Table 2.

*, ** Correlation significant at 0.05 and 0.01, respectively.

elevation gradients and enhances the productivity and ability of these populations to adapt to new conditions (LAST et al., 2014). According to the coefficient of correlation, LA is correlated with LW and PL. The different kinds of correlation among different leaf traits in beech (BAYRAMZADEH et al., 2008) and other species were also reported by other authors (YOUSEFZADEH et al., 2010, RAKONJAC et al., 2014; ALLAHNOURI et al., 2018). The high heritability indicated that the effect of genotype is more important than the environmental pressures. Most of the traits treated in this study displayed a high heritability and, consequently, they may be considered as better and more correct choices for the breeding programs. High genetic variation reflects an increase in heterozygosity at the stands progeny, which increases the future sustainability of ecosystems facing with the global change and adaptability. Furthermore, genetic diversity among populations is an important factor for adaptive assessment of diversity. Another studies showed a high genetic diversity among *Fagus orientalis* Lipsky populations in Iran (SALEHI SHANJANI et al., 2012). The low heritability ratio can be due to low-quality alleles, a low genetic variation or a gene-environment interaction. The low coefficient of genetic and phenotypic variation in specific leaf area (SLA) indicated that these traits are less compatible with the environmental conditions. This result is in line with the finding of other studies such as BRENDEL et al., 2008; ZOLFAGHARI et al., 2013. Differences in plasticity were found among the populations. In this study, RWC showed the highest plasticity. This result is in consistence with the findings of POULOS et al (2012) who observed that the differences within populations can be a result of micro-ecosystem conditions, which was experienced by each tree or due to the genetic differences among the individuals. The results of this study suggest that the middle elevation (1,200m) can be the optimum zone for growth and development of *Fagus orientalis*. The traits showing the highest plasticity are the most important for leaf function in different environments and these trait have also more ability for adaptation.

Conclusion

This study was conducted to investigate the genetic variability and heritability of some morphological and physiological traits in *Fagus orientalis* Lipsky along an elevation gradient in Hyrcanian forests. The results of this study revealed that leaf traits can be influenced by climate change along elevation gradients, and that these traits can adapt to new conditions. Therefore, in order to achieve more reliable results and to recognize the compatibility of *Fagus orientalis* in response to climatic changes, molecular studies are required based on the traits showing the maximum and minimum plasticity in response to elevation changes.

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