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INTER – AND INTRAPOPULATION VARIATION OF LEAF MORPHOLOGICAL TRAITS IN NATURAL STANDS OF *BUXUS HYRCANA* (POJARK.) IN CASPIAN FORESTS (IRAN)

ABSTRACT: The leaf morphology of *Buxus hyrcana* (Pojark.), shade-tolerant and evergreen species growing in understorey of Caspian Forest was studied in five natural Iranian populations in order to recognize the pattern of within- and among-population variation of selected leaf morphological traits. Fifteen traits were selected and measured or calculated – list in Appendix. Leaves were collected from different geographical (between 36°13′N and 53°15′E) populations of *B. hyrcana* growing in the Caspian Forests located in Mazandaran Province (northern Iran) in the similar vegetation and site conditions but on different altitudes. Ten mature trees from five relatively small areas (0.5–1 ha) were selected in June. Then ANOVA model was used with both crossed and nested effects. The results showed that variation among the populations was significant in 13 of 15 traits (P <0.05); variation among the trees in the population was significant in 14 of 15 traits (P <0.05). Among all characters measured, the greatest plasticity was found for weight, leaf area mass and specific leaf mass. Function 1 explained 30% of the total variance and Function 2 represented another 17% of the total variance. PCA analysis showed that the most important role in function 1 allocated to width of lamina and *leaf figure* ratio (length of lamina/width of lamina) and in function 2 to *top of leaf figure* (width of lamina in 0.1 its length/width of lamina). The results of the average linkage clustering method evidenced four distinct clusters. Generally, morphological traits of leaves of *B. hyrcana* showed low variation among the considered populations based on clustering analysis, although some trees inside the population showed significantly different values in comparison with other trees.

KEY WORDS: *Buxus hyrcana*, leaf morphology, plasticity, specific leaf area

1. INTRODUCTION

Resource availability and environmental conditions may influence the distribution and functional characteristics of the species inhabiting a region (Beadle 1966, Ko¨rner *et al.* 1989). Many species have a wide geographical distribution and therefore their individuals have to thrive under contrasting environmental conditions (Castro *et al*. 1997). Most of the intraspecific studies have revealed that many plant characteristics (morphological and physiological) can change under different growing conditions (Bissing 1982, Woodward 1983, Baas *et al.* 1984, Waring 1991, Karlsson 1992). Plant leaves are an important interface to the environmental factors, such as temperature, sunlight and relative humidity. Some morphological characters of leaf *e.g.* leaf area and leaf thickness are strongly modified by ecological conditions (Mclellan and Endler 1998; Bruschi *et al.* 2003; Harris *et al.* 2003). Great leaf variability that exists among taxa and among individuals within the same taxon may overwhelm our perceptions of variability within individual plants. However, a high degree of variation among vegetative characters within trees was evident in many studies (De Rivas 1972, Baranski 1975, Olsson 1975, Sokal *et al.* 1986, Blue and Jensen 1988). Changes of features of leaves could be a part of adaptation responses in face to the factors, such as light intensity and water supply (Groom and Lamont 1997). Specific leaf mass (dry weight: leaf area ratio, SLM) can be related to water and carbon economy, but there is no single causal factor to explain its variation. Numerous studies have related differences in SLM among species to change in the proportion of support and photosynthetic tissue (Garnier and Laurent 1994, Van Arendonk and Poorter 1994), high SLM being related to low nitrogen content (Field and Mooney 1986, Turner 1994), to low photosynthetic potential (Field and Mooney 1986, Reich *et al.* 1992) and to low growth rate (Lambers and Poorter 1992). However, SLM variations induced by different light regimes within a species seem to be the consequence of changes in the palisade parenchyma thickness, high SLM being associated with high nitrogen content per unit of leaf area, and with a high photosynthetic rate (Chabot and Chabot 1977, Jurik 1986).

Ecological gradients, such as altitude, influences leaf structural traits at intraspecific level (Bussotti *et al.* 2005). We expect that SLM changes, induced by aridity within a species, would be more related to the amount of support tissue than to the mesophyll development, thus being positively correlated with fiber and negatively with nutrients.

Buxus hyrcana (Pojark.) is a shade-tolerant and evergreen species growing in understorey. It has occupied a large range from plain to up to 1000 meter above sea level in Caspian Forests, northern Iran (Sabeti 1984). Natural populations of *B. hyrcana* are rapidly disappearing due to illegal logging and deforestation associated with conservation of lands for agriculture, fruit culture, pasture and precious wood. Establishing a forest genetic resource conservation program for protecting the remaining within-species genetic diversity first and foremost requires information on the patterns of genetic variation among and within populations (Saenz-Romero *et al.* 2006). This information is basic to deciding, for example, the size and location of Forest Genetic Resource Conservation Units (Saenz-Romero *et al.* 2006), also called forest genetic resource management units (Millar and Libby 1991).

The aim of this study was therefore to investigate the influence of altitude on leaf morphology of *B. hyrcana* species and to recognize whether the responses (plasticity) of the traits differed along altitudinal gradient.

2. STUDY SITES

Leaves were collected from five populations of *Buxus hyrcana* (Table 1) in the Caspian Forests located in Mazandaran Province,

Table 1. Characteristics of the study areas.

Code	Locality	Latitude	Longitude	Altitude (m)	Forest Type	Soil Type
SH	Shirgah	36°34′44″	52°14′36″	420	*Carpinus betulus – Buxus hyrcana*	Brown Calcareous
A	Atto	36°14′17″	52°59′60″	570	*Carpinus betulus – Buxus hyrcana*	Brown Calcareous
S	Sangneshast	36°13′93″	52°59′99″	834	*Carpinus betulus – Buxus hyrcana*	Brown Calcareous
P	Pejet	36°15′23″	53°39′29″	1100	*Carpinus betulus – Buxus hyrcana*	Brown Calcareous
GH	Gharansara	36°12′57″	53°10′07″	1200	*Carpinus betulus – Buxus hyrcana*	Brown Calcareous

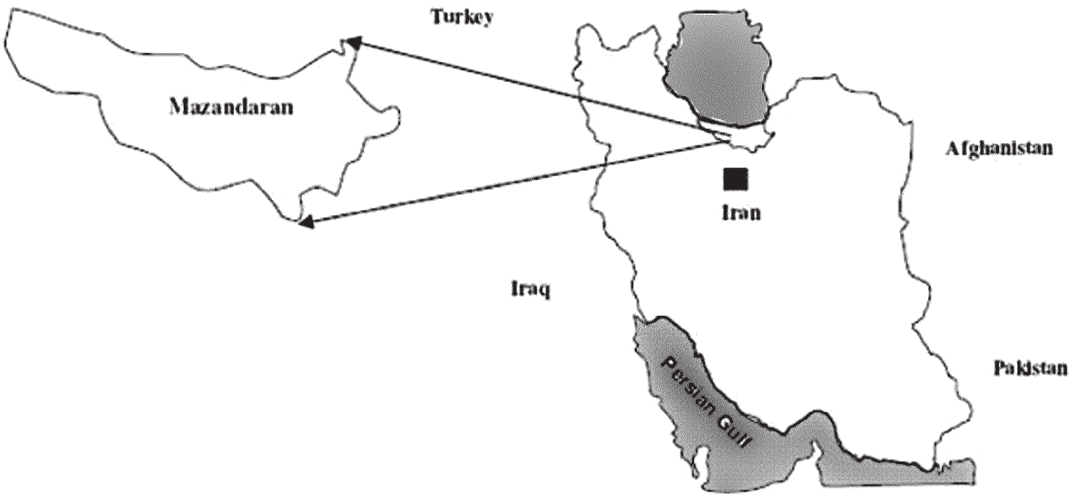

Fig. 1. Position of the study area in the north of Iran.

north of Iran, between 36°13′N and 36°15′N and 53°10′E and 53°15′E (Fig. 1). Populations are dispersed across an elevation range (10–1200 m) (Table 1); average distance between them was about 50 km. The mean air temperature varied between 6.8°C being the lowest in Gharansara and 12.5°C being the highest in Shirgah. The mean annual rainfall varied from 1230 mm in Pejet to 1850 mm in Shirgah. The tree vegetation type in all sites was dominated by hornbeam (*Carpinus betulus*), with *Buxus hyrcana* in understorey. The limestone composed the bedrock of all populations with brown calcareous soil type (Table 1).

3. METHODS

Firstly, 10 mature trees from a relatively small area (0.5–1 ha) were selected in each site. The height of trees was in the range of 3–14 m. Four outermost branches were randomly selected from the crown of each tree in June, due to higher vitality and health of leaves in this month. Branches were collected from the four cardinal compass directions, avoiding lammas and epicormic shoots. Forty fully expanded leaves of current year and eight twigs were randomly selected from each subsample after elimination of broken, incomplete or damaged units. The leaves were practically of the same age, although there was a small variation in budburst both among trees and within trees. The list of traits analyzed is reported in Appendix. The total surface area was measured with a LI-COR LI–3100 Leaf Area Meter on 10 leaves stripped of the petiole for each subsample. Afterwards, these leaves were dried at 70°C for 72 hours and leaf mass per area was calculated as the dry weight (mg) divided by lamina area (cm^2). All data were subjected to statistical analysis to determine the mean values and analyzed using analysis of variance (ANOVA), simple correlations, and other treatments. Assumptions of normality were checked with Shapiro-Wilk's test. Normality of characters distribution was assessed for all variables. To test the main effects of population (P), tree within population (T) and their interaction (T × P) were analyzed. Homogeneity of variances was tested in all levels with the Bartlett test (Sokal and Rohlf 1995). Total within-population plasticity (Pl) was calculated for each population and each measure using the smallest and the greatest mean values:

$$Pl=1-(x/X) \qquad (1)$$

Where x is the smallest value and X is the largest value for any given leaf measure (Ashton *et al.* 1998).

Duncan's multiple range test was used for grouping the parameter means (Steel and Torrie 1980). An ordinal ranking scheme was instituted to show the provenance score for each parameter to indicate the overall provenance performance. The analyses of variance were conducted with SPSS software, vers. 12.5 (SPSS, Chicago, IL, USA). The average Linkage program was used to compute cluster groupings of *B. hyrcan*a populations, according to leaf morphology characteristics using the JMP Program, vers. 3.1.2. The average linkage distance is the average distance between pairs of points in each cluster (Oleksyn *et al.* 2001). A principal components analysis (PCA) was applied to identify which leaf traits represent gradients of maximum variation within a data set (McGarigal *et al.* 2000). A PCA is concerned with explaining the variance structure through a few linear combinations of the original variables (Johnson and Wichern 1982).

4. RESULTS

All hierarchical levels (populations, trees within population and interaction between branch tree and population) contributed significantly to variation in *B. hyrcan*a foliage (Table 2). Variation due to populations was significant in 13 of 15 traits (P <0.05); varia-

Table 2. Mean values of the leaf traits (see Appendix) for five populations of *B. hyrcana* (SH, A, S, P, GH, – see Table 1), mean values of the plasticity index (Pl) (see formula 1) and CV – coefficient of variation in % of mean value. The same letter in the same row indicates not significantly difference (P >0.05), according to Duncan's test.

Morphological characters	Population											
	SH		A		S		P		GH		Pl*	C.V. (%)
	Mean	Pl	Mean	Pl	Mean	Pl	Mean	Pl	Mean	Pl	Mean	
LP	2.65 b	0.75	2.86 ab	0.5	3.06 a	0.6	2.86 ab	0.8	2.73 ab	0.5	0.63	5.1
LL	27.5 a	0.44	22.93 b	0.53	22.92 b	0.7	22.06 b	0.56	25.7a	0.72	0.59	8.9
WL	12.27 a	0.43	9.33 c	0.27	10.66 b	0.58	10.69 b	0.53	11.73 a	0.53	0.46	10.3
WL (0.1)	5.65 ab	0.55	4.04 c	0.4	5.24 b	0.62	5.24 b	0.62	6.04 a	0.66	0.57	14.2
WL (0.9)	6.5 a	0.55	4.86 b	0.33	5.44 b	0.42	6.15 b	0.55	6.68 ab	0.7	0.51	12.1
BA	67.5 b	0.39	61.6 d	0.26	63.06 c	0.56	62.61 b	0.43	65.02 a	0.49	0.42	3.6
NPV	26.22 ab	0.3	22.13 b	0.24	22.62 b	0.5	20.43 c	0.48	25.2 a	0.39	0.38	10.1
LF	2.3 a	0.52	2.45 a	0.41	2.19 b	0.6	2.08 b	0.61	2.19 b	0.75	0.58	6.2
ELF	0.46 bc	0.4	0.43 c	0.46	0.49 ab	0.49	0.49 ab	0.55	0.5 a	0.38	0.45	6
TLF	0.49 b	0.46	0.52 b	0.36	0.53 b	0.53	0.57 a	0.53	0.56 a	0.38	0.45	6
LPR	2.59 b	0.43	2.81 b	0.44	2.84 b	0.57	3.11a	0.54	2.61b	0.52	50	7.5
Productivity measures		0.47		0.38		0.56		0.56		0.54	0.52	8.18
W	0.031	0.82	0.026	0.6	0.032	0.71	0.03	0.82	0.03	0.82	0.75	7.65
LA	212	0.52	179.4	0.35	275.1	0.61	200.5	0.75	188.5	0.63	0.57	17.9
SLM	1.52	0.76	1.46	0.45	1.2	0.71	1.64	0.94	1.66	0.79	0.73	12.3
Means		0.71		0.48		0.7		0.85		0.76	0.7	12.61

* average plasticity for each character recorded among 5 populations.

Table 3. Regression equations between leaf traits (see Appendix for codes) and altitude of populations (Table 1).

Leaf trait	relationship	R
LP	0.04E-03X+3.3	-0.23
LL	0.0083X+16.24	**0.44***
WL	0.0035X+7.6	**0.48***
WL (0.1)	0.029X+3.07	**0.56****
WL (0.9)	0.0023X+3.16	**0.76****
BA	0.0055X+57.98	0.28
NPV	0.0053X+18.26	**0.52***
LF	0.01X+184.4	0.25
TLF	0.0002X+2.36	0.24
ELF	-2E-05X+1.07	-0.08
LPR	8E-05X+0.14	0.39
SLM	-3E-05X+0.014	-0.34
W	-3E-05X+0.06	0.05
AREA	-0.0042X+18.84	-0.005

* significant at the 0.05 level ** significant at the 0.01 level

tion due to trees inside the population was significant in 14 of 15 traits ($P<0.05$); and variation due to interaction between population and tree within population was significant in all of 15 traits ($P<0.05$) (Table 2).

Correlations among leaf features and altitude of populations are represented in Table 3. Length of lamina (LL), width of lamina (0.1, 0.9) (WL), and number of principal vein (NPV) were positively correlated with altitude of populations.

Of all characters measured, greatest plasticity was found for productivity traits (0.7). Particularly, dry weight (DW) and specific leaf mass (SLM) showed very high values: 0.76 and 0.73, respectively (Table 2). The differences among populations were not high. Measures of plasticity for macromorphology were consistently about the same among populations. Plasticity of number of principal vein (NPV) and base angle (BA) was relatively low. Total pattern of variation showed that G (Gharansara,), P (Pejet) and S (Sangneshast) populations were the most plastic (Table 1), while A (Atto) population was the least plastic. SH (Shirgah) population was intermediate between these two groups. Also, the results indicated that the productivity measures had greater coefficient variation than macromorphological characters, so that the leaf area (LA) had maximum coefficient of variation (Table 2).

To investigate multivariate associations among the measured characters, a principal component analysis (PCA) was performed on data for all populations. Results of PCA analysis showed that five of the seven roots had a significant associated eigenvalue. Traits highly correlated with each of the five functions are reported in Table 4. Leaf weight and 'leaf figure' were in function 1, 'top of leaf figure' and weight of leaf - in function 2, specific leaf mass - in function 3, 'end of leaf figure' and leaf petiole ratio - in function 4, and 'area'- in function 5 denoted from PCA analysis.

A cluster analysis classification technique was used to group populations according to

Table 4. Leaf traits (codes in Appendix) of the *B. hyrcana* trees used in principal components analysis and the contribution of the first four components, at 5% probability level*.

	Principal component				
Eigenvalue	4.5	2.57	2.01	1.39	0.99
Total Variance (%)	30	17.1	13.4	9.3	6.6
Cumulative Total Variance (%)	30	47.1	60.1	69.9	76.5
Anatomical characters					
LP	-0.09	-0.34	-0.22	-0.18	0.36
LL	-0.27	-0.38	-0.05	0.29	0.09
WL	-0.45*	0.04	0.02	0.13	-0.002
WL (0.1)	-0.38	-0.05	0.29	0.03	0.28
WL (0.9)	-0.35	0.15	0.32	0.05	0.12
BA	-0. 34	0. 18	-0. 09	-0. 17	-0. 30
NPV	-0.26	-0.39	-0.14	-0.10	-0.11
LF	-0.36*	-0.002	0.06	0.15	-0.48
TLF	0.17	-0.46*	-0.05	0.16	-0.02
ELF	0.22	-0.06	0.19	0.44*	-0.25
LPR	0.02	-0.04	0.4	-0.55*	0.21
W	-0.02	0.46*	-0.18	0.13	0.19
AREA	0.07	0.06	0.41	0.47	0.03
SLM	0.10	0.25	0.35*	0.16	-0.5

characters measured. An average linkage clustering method, are summarized in a dendrogram (Fig. 2). Four distinct clusters were identified. Tree number S19 and S20 from Shirgah population and P6, P11, P13 from Pejet population comprised groups (clusters) of 1, 2 and 3, alone. The other trees comprised group 4. Maximum distance was observed between tree number 1 and tree number 19 from Pejet and Sangneshast populations, respectively. Also the minimum distance was found 31 and 44 from Shirgah and Gharansara populations, respectively.

5. DISCUSSION

Results clearly demonstrate the high phenotypic diversity of the *Buxus hyrcana* population (Table 2). Several measured leaf parameters differed significantly among populations and among trees within the same population. The high variability, at individual and population level is a usual finding (Castro *et al.* 1997, Coelho *et al.* 2002, Bruschi *et al.* 2003, Tabari *et al.* 2008). However, several species have been found to show little variation at these levels and sometimes different populations of the same species may have different patterns of variation (Rambal and Leterme 1987, Mulkey *et al.* 1993). Environmental heterogeneity represents an extrinsic source of within-population variation. Variability in the light or microclimate encountered by different plant structures can affect leaf characteristics.

Generally, for plants of the same species, high values of specific leaf mass (SLM) are

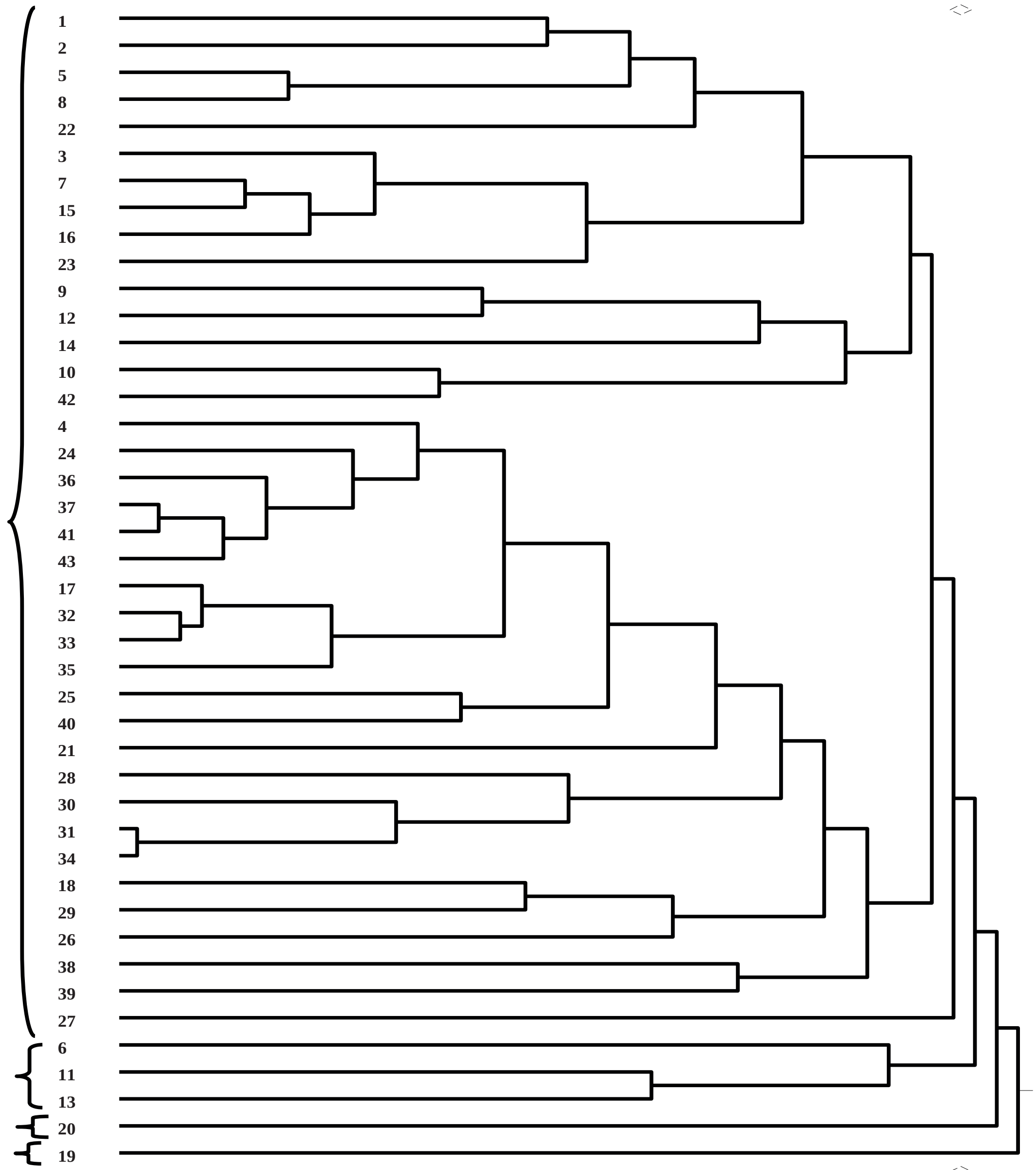

Fig. 2. Dendrogram of cluster grouping of populations of *B. hyrcana*, based on leaf characters measured in trees. No. 19 shows number of tree from population of SH (Shirgah) and represents cluster 1. No. 20 shows number of tree from population of SH (Shirgah) and represents cluster 2. No. 6, 11 and 13 show number of tree from population of P (Pejet) and represent cluster 3. Other numbers show number of trees from all populations and represent cluster 4.

related to high intensity of light (Osunkoya and Ash 1991, Mulkey *et al*. 1993, Kitajima 1994, Muraoka *et al*. 1997). This response is related to increased thickness of the leaf tissues (Hanson 1917), especially the palisade parenchyma (Fretz and Dunham 1972). SLM increased linearly with light and therefore it may be considered a species-specific estimate of long-term light conditions (Niinemets 1997). Diminished water supply can contribute to the increase of SLM in some cases (Groom and Lamont 1997), while in others no difference was observed (Mulkey *et al*. 1993). Among all the parameters, SLM appeared to be the most suitable for highlighting the ecological differences between the stands (cf. Castro-Díez *et al*. 1997, Bussotti *et al.* 1997), although straightforward inference is difficult. SLM is influenced by leaf thickness and leaf density (Witowski and Lamont 1994) but these parameters can have a different ecological meaning (Givinsh 1979).

The leaf area (LA) is negatively correlated with the light intensity, when comparing plants of the same population or leaves from the same tree (Crawley 1997, Kozlowsky and Pallardy 1997). Roderick *et al.* (2000) used models and data from various species of *Eucalyptus* to demonstrate that leaf area, and hence leaf size, is influenced by a combination of nutrients and water availability. Further, McDonald *et al.* (2003) demonstrated that water availability and soil phosphorus were independently related to leaf size in 690 species at 47 sites.

In this research, 'base angle' parameter had the lowest coefficient variation and plasticity along various sites. This result confirms the tolerance of *Buxus hyrcana*, because change of base angle is a response to a more shaded environment, so that decrease of base angle of leaf can increase the proportion of area on the lamina apical half, amplifying the exposure to light. The greater length of the petiole observed in sun leaves can have an important effect on the spatial distribution of leaves and therefore on light interception populations. Also, large differences were observed among the macro-morphological and productivity traits in all populations. In reality, the productivity traits showed large plasticity among different populations. This indicated that the productivity parameters are more affected by environmental conditions. Interspecific studies have also shown a decrease of leaf area and an increase of SLM with aridity (Goble-Garratl *et al.* 1981, Specht and Specht 1989, Floret *et al.* 1990). All these data suggest that this evergreen species relies on its foliage plasticity and physiology to overcome water shortage, which can be studied precisely in future. Generally, studying morphological traits of leaves of *B. hyrcana* based on clustering analysis showed low variation among populations under study, although some trees show different values in comparison with other trees.

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APPENDIX

LIST OF MORPHOLOGICAL AND ANATOMICAL CHARACTERS

Anatomical characters	Macromorphologicl measures
LP:	Length of petiole (mm)
LL:	Length of lamina (mm)
WL:	Width of lamina (mm)
WL (0.1):	Width of lamina in 0.1 its length (mm)
WL (0.9):	Width of lamina in 0.9 its length (mm)
BA:	Base angle
NPV:	Number of principal vein
Calculated measures	
LF:	Leaf figure (lamina length/lamina width)
TLF:	Top of leaf figure (lamina width at 0.1 its length /lamina width)
ELF:	End of leaf figure
LPR:	Leaf petiole ratio
Productivity measures	
W:	Weight of leaf (g)
LA:	Leaf area (cm^2)
SLM:	Specific leaf mass (mg/cm^2)