

## Climatic Conditions and Herbivory Effects on Morphological Plasticity of *Argania spinosa*

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The main objective of this paper was to look into the morphological differentiation patterns and phenotypic plasticity in four populations of *Argania spinosa* with environmentally contrasted conditions. Mean response, magnitude and pattern of morphological intra- and inter-population plasticity indexes were measured and analyzed in order to identify which characters contribute the most to the acclimation of this species. Populations growing in the ecological optimum of the species presented the lowest plasticity, while those growing in the most stressed habitats showed an increased morphological variability. The study of four populations showed that human pressure seems to play an important function in the regulation of morphological characters. However, climatic conditions seem to play a significant role in the increase of morphological plasticity.

**Keywords:** Crown structure, LMA, LAI, Plasticity index.

To estimate environmental stress in plants, ecologists use instantaneous measurements such as leaf water potential, photochemical efficiency, and CO<sub>2</sub> assimilation rate. However, morphological data such as tree height, diameter, volume and growth are integrative physiological measures at longer scales and may be used as surrogate analysis of fitness [1].

The morphological variability in populations of a single species can be explained by a simple acclimation to different environments. Plants of the same species usually grow in habitats with different environmental conditions to which they are particularly adapted, frequently with genetic differences [2]. In the case of trees, they harbor high levels of genetic diversity and can adapt rapidly to either local or new conditions [3]. The capability of a given genotype to give rise to a range of phenotypic expressions under different environments is known as phenotypic plasticity [4]. Trees have been described to have high morphological and physiological plasticity [3]. Usually, morphological variables have been used to quantify the phenotypic plasticity and to make comparisons between species [5], although few plant species have been studied.

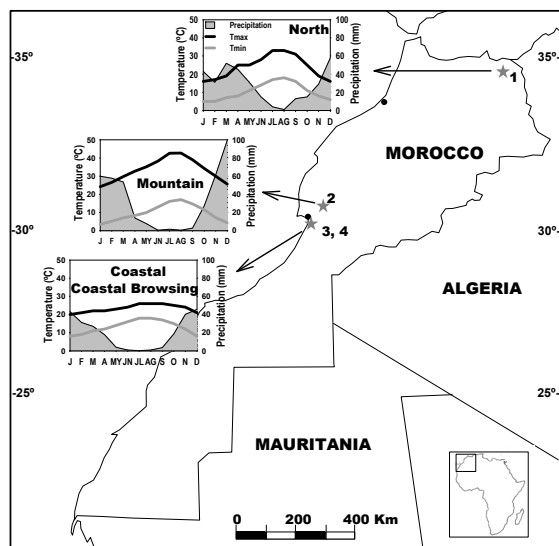
*Argania spinosa* is the only endemic species of the tropical family *Sapotaceae* naturally present in Morocco. An excessive zoo-anthropological action is leading to the absence of natural regeneration of this species [6,7]. Human pressure is slowly, but continuously, degrading and destroying important extensions of argan ecosystems [8,9]. De Waroux & Lambin [10] confirmed that argan woodlands in SW Morocco underwent a dramatic 40% density decline between 1970 and 2007.

It has been shown how high phenotypic plasticity increases survival possibilities in new environmental conditions, or when stress conditions or perturbations occur [11]. *A. spinosa*'s biogeographical range is affected by stressing conditions, mainly due to water scarcity and high water loss by evapotranspiration, but also due to the herbivory pressure on its range area.

The main objective of this study was to look into the morphological differentiation traits and phenotypic plasticity between four populations of *A. spinosa* with environmentally contrasted conditions. Mean response, magnitude and pattern of morphological intra- and inter-population plasticity index were measured in order to analyse which characters were more plastic, and contributed the most to the acclimation of this species. Four study areas, with either different herbivory intensity or climatic conditions, were selected:

**1. Douar Chwihiya** (hereafter North). Douar Chwihiya is a small village close to the Beni Snassen Mountains. The study area is located on a north oriented smooth slope, close to the coastal plane, at an altitude of 210 m (Figure 1). Vegetation is an open forest, where *A. spinosa* is accompanied by pines (*Pinus halepensis*) and wild olive trees (*Olea europaea*). Until the settlement of a protection fence within a Government preservation program two years before the study, the area had been used for goat pasture, which promoted the presence of nitrophyllous species and prevented the natural regeneration of the argan forest. Apart from argan trees, other shrub species are *Genista ferox*, *Whitania frutescens*, *Rhus pentaphylla*, *Ziziphus lotus*, *Launaea arborescens*, *Lavandula dentata*, *Marrubium vulgare* and *Thymus maroccana*. The climate is Mediterranean, with 337 mm of annual rainfall, concentrated from September to May. Monthly average temperatures are 30°C in summer and 5°C in winter. Relative humidity ranges between 58-60% in summer and 65-75% in winter. This population was selected for its intermediate climatic conditions and for its isolation, 800 km apart from the species' main distribution area.

**2. Tassademt** (hereafter Mountain). Located 70 km NE of Agadir, in the first foothills of the Atlas Mountains. The studied population grows on a slight slope at 810 m of altitude. The argan forest is the predominant vegetation type (Figure 1). Woody vegetation is scarce and scattered, mainly composed of spiny shrubs, like *Genista ferox*, *Launaea arborescens* and *Ziziphus lotus*, but also non-spiny species



**Figure 1:** Location and ombrothermic diagram of the 4 studied areas: 1 North; 2 Mountain; 3 Coastal Browsing; 4 Coastal.

like *Periploca laevigata* and *Ephedra fragilis*. The climate is more extreme than in Agadir, with marked continental character. Monthly average temperatures are 40°C in summer and 3°C in winter (Figure 1). However, it can drop to -5°C. Rainfall is scarce (385 mm yearly) and concentrated from October to April, which, combined with high temperatures, make summer droughts especially severe. Relative humidity in this population was the lowest of all four (from 40-50% in summer to 60-70% in winter). The extreme climatic conditions, close to the distribution limit of the species, were the reason for its selection.

**3. Admine Forest** (hereafter Coastal Browsing). Located in the suburbs of Agadir, 107 m of altitude, in a strongly humanised area, traditionally managed for agriculture and livestock raising. The argan forest is a very much cleared community. Argan trees show broken and cut branches and some that have been cut down appear to be resprouting. Apart from argan trees, natural vegetation is scarce: *Acacia gummifera*, *Euphorbia beaumeriana*, *Ziziphus lotus*, *Asparagus pastorianus*, *Launaea arborescens*, *Periploca laevigata*, *Bupleurum mezereum* and *Whitania frutescens*. The climate is temperate due to marine influence, with maximum temperatures never surpassing 30°C, and the minimum never below 7°C. Annual rainfall is scarce -232 mm- and concentrated from October to April (Figure 1). Relative humidity in this population was the highest of all four (from 65 to 75% throughout the year). This area is considered [12] to be the ecological optimum of the species and the centre of its distribution area. The Admine forest population was selected by the high intensity of herbivory pressure, mainly by goats.

**4. Houbara Sanctuary** (hereafter Coastal). The sanctuary is a protected area for the reproduction of the African great bustard (*Chlamydotis undulata*). Human activity has been restricted for the last 18 years in this natural argan forest, which is located to the south of Agadir, 8 km from the Coastal browsing population. Except for human pressure, environmental conditions are similar.

To estimate livestock pressure, the number of goat droppings beneath and outside *A. spinosa* trees was counted in 20 plots, each of 0.5x0.5 m area.

Eleven traits were measured to detect morphological changes as a function of their environment. All variables were measured in April

in 20 randomly chosen trees in each population (except in Coastal, where 15 trees were measured).

1. Leaf area index (LAI) was calculated through the luminic radiation attenuation method, using a LAI-2000 Plant Canopy Analyzer device, from Licor (USA). Two outer radiation measurements were compared with 10 inner ones, following five different azimuthal angles [13].
2. Leaf area. Five fully expanded leaves of 20 well-developed trees (3-4 m height) were collected from the upper sun-exposed crown (100 leaves per site). Leaf area was calculated after scanning with image analysis software Midebmp [14].
3. Leaf mass area (or sclerophyll index). After being scanned for leaf area, leaves were dried, weighed, and the ratio leaf mass/leaf area calculated (LMA,  $g \cdot m^{-2}$ ).
- 4, 5. Tree and crown heights were measured with a laser Impulse 200 LR clinometer (Laser Technology Inc, USA).
6. Crown projection area (cover) was calculated using the maximum and minimum orthogonal diameters of the canopy's vertical projection, whose shape approached being elliptical.
7. Crown volume was estimated by similarity to geometric figures [15] from height and diameters data, approaching its shape to one half of a revolution ellipsoid, using the formula:  $Vol = 1/2 (4/3 \pi * r_1 * r_2 * r_3)$ , where radii 1 and 2 are one half of the crown projection diameters and radius 3 is equal to crown height.
8. Trunk perimeter was measured 5 cm above the ground (as branches grow from the base in most individuals).
9. Crown sphericity ( $C_{sphericity}$ ) was calculated as the ratio of crown height to crown average diameters. Values near 1 indicate spherical crowns, while values near 0 indicate flat crowns.
10. Crown asymmetry ( $C_{asymmetry}$ ) was calculated as the ratio of maximum to minimum diameter. Values near 1 indicate symmetry; the more distant to 1, the more asymmetric the crown.
11. Crown/tree height ratio was computed as crown height per total tree height (CTHR). Values near 1 indicate crown growth from ground level, while values near 0 indicate a small crown with respect to total tree height.

An index of plasticity (ranging from 0 to 1) was calculated following Valladares *et al.* [16] for each of the 11 morphological traits as the difference between the maximum and the minimum values divided by the maximum one. Values near 0 indicate homogeneity in character, while values near 1 indicate a large variability. Morphology plasticity index was calculated within each population (intra-population) taking maximum and minimum values among individuals within a population, and between populations (inter-population), taking these values among individuals from the pooled data of the four populations.

Differences in morphological traits between populations were tested by means of a one-way ANOVA. Post-hoc Tukey test was used to compare pairwise differences. Except for crown projection, which was Ln transformed, the data fitted normal distribution. Analyses were performed using SPSS 14.0 for Windows software.

As expected, the number of droppings was significantly different between populations ( $F_3=52.0$ ,  $p<0.001$ ); their densities were always higher beneath than outside *A. spinosa* canopies ( $F_1=27.4$ ,  $p<0.001$ ). Coastal Browsing was the site with the highest droppings density, indicating the highest level of herbivory pressure, while Coastal and North sites had no droppings at all, as livestock access is restricted (Figure 2).

LAI differences between populations were significant in spring and summer (Figure 3, Table 1), and in both cases with the same pattern, North and Coastal populations with the highest values 3.5

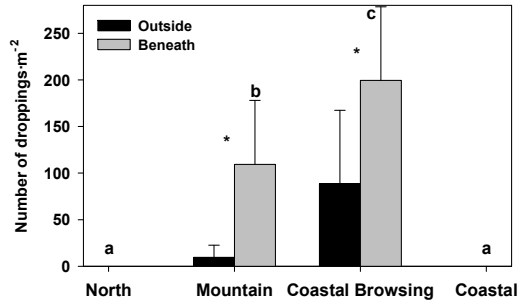


Figure 2: Goat dropping density beneath and outside of *A. spinosa* at the 4 study sites. (Mean  $\pm$  sd, n= 20). Lower-case indicates post hoc Tukey test results. \* indicates significant differences within populations.

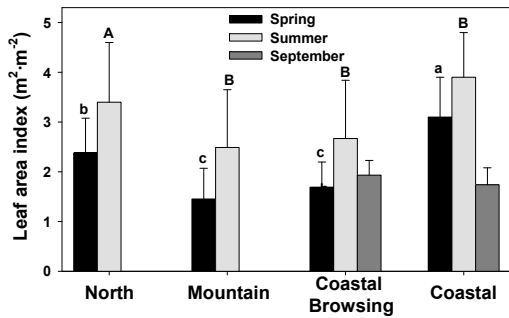


Figure 3: Mean leaf area index (LAI)  $\pm$  sd at the 4 study sites. Lower-case in spring and capital letters in summer indicate Tukey test results.

Table 1: One-way ANOVA results on the effects of population for morphological variables (post hoc Tukey test included in figures 2-7).

	fd	SM	F	P
Leaf area index	3	9.08	19.88	0.001*
Leaf area	3	599.1	9.06	0.001*
Leaf mass area	3	2607.2	4.35	0.007*
Tree height	3	6.08	4.01	0.011*
Crown height	3	12.80	12.10	0.001*
Major diameter	3	42.34	6.92	0.001*
Minor diameter	3	47.91	8.23	0.001*
Crown projection	3	9.10	10.78	0.001*
Crown volume	3	63571.5	4.58	0.005*
Trunk perimeter	3	0.58	0.90	0.444
Crow <sub>sphericity</sub>	3	0.14	6.92	0.001*
Crow <sub>asymmetry</sub>	3	0.279	2.69	0.05*
Crown-tree Ratio	3	0.14	11.04	0.001*
Plasticity index	3	0.18	5.46	0.003*

\* indicates significant differences.

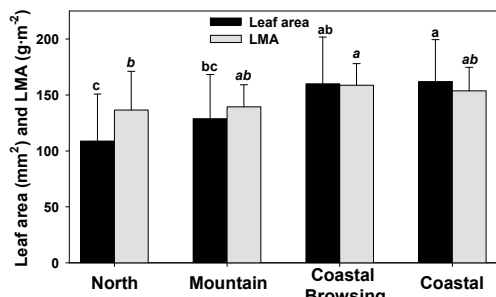


Figure 4: Mean leaf area and leaf mass area (LMA)  $\pm$  sd at the 4 study sites. Lower-case indicates post hoc Tukey test results.

and 3.9  $m^2 \cdot m^{-2}$ , respectively) opposed to Mountain and Coastal Browsing with the lowest (2.5 and 2.7  $m^2 \cdot m^{-2}$ , respectively). In September, only 2 populations could be measured, Coastal showing the lowest value of the year (1.7  $m^2 \cdot m^{-2}$ ).

One-way ANOVA revealed differences in leaf area and LMA (Table 1). Coastal and Coastal Browsing populations had the biggest leaves (162-160  $mm^2$ ), while the highest LMA was

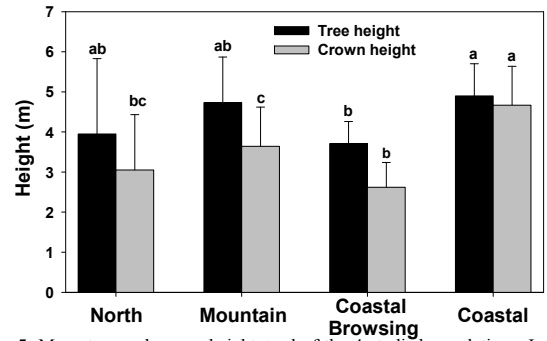


Figure 5: Mean tree and crown height  $\pm$  sd of the 4 studied populations. Lower-case indicates post hoc Tukey test results.

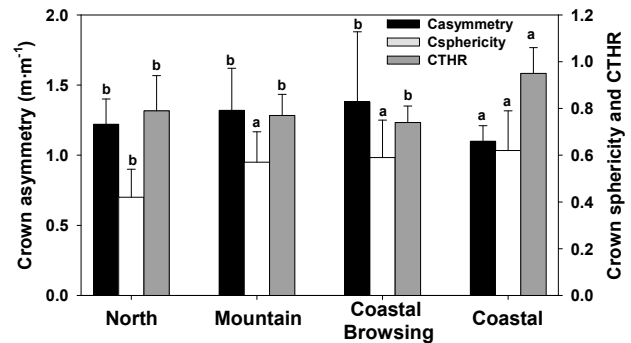


Figure 6: Mean  $C_{asymmetry}$  (maximum/minimum crown diameters),  $C_{sphericity}$  (crown height/mean crown diameters) and CTHR (crown/tree height)  $\pm$  sd at the 4 study sites. Lower-case indicates Tukey test results.

measured in the Coastal Browsing population (158  $g \cdot m^{-2}$ , Figure 4). In contrast, the smallest leaves with the lowest LMA were measured in the North population (108.8  $mm^2$  and 136  $g \cdot m^{-2}$ ).

Tree and crown height,  $C_{asymmetry}$  and  $C_{sphericity}$  were significantly different between populations (Table 1). Trees from Coastal were the tallest (5 m), and they had the most spherical (0.62  $m \cdot m^{-1}$ ) and symmetrical crowns (1.1  $m \cdot m^{-1}$ ). Contrarily, Coastal Browsing trees, in spite of the close vicinity to Coastal populations, were the smallest (3.71 m tall), and had the most asymmetrical crowns (1.38  $m \cdot m^{-1}$ ), although they had similar sphericity values (Figure 5, 6).

Trunk perimeter was not different between populations, ranking from 1.3 m in Coastal Browsing to 1.68 m in Coastal (Table 1, Figure 7). Trees from North and Coastal exhibited bigger crown cover (50.3 and 46.6  $m^2$ , respectively) than Mountain and Coastal Browsing (this population had the smallest crown cover, 12  $m^2$ ).

The less plastic variables were LMA, CTHR and  $C_{asymmetry}$ , while crown cover and volume were the most plastic attributes (Table 2). Trees from North and Mountain populations presented the highest variability in almost all the measured variables (except  $C_{asymmetry}$ ), which ranked from 0.41 to 0.99. On the other hand, trees from Coastal population showed the lowest variability in most of the morphological traits, ranking from 0.30 in trunk perimeter to 0.64 in LAI.

Argan populations varied for each particular morphological trait measured, except for trunk perimeter, for which there were no differences between the populations (Table 1).

In order to have an integrating measure, morphological plasticity index was calculated as the mean of the variability of the 11 morphological traits (Figure 8). Trees from North and Mountain

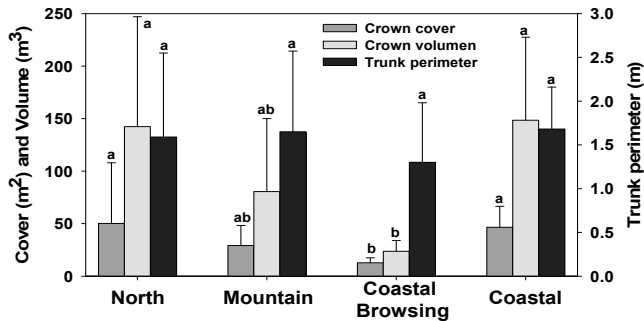


Figure 7: Mean crown cover (m<sup>2</sup>), volume (m<sup>3</sup>) and trunk perimeter (m) ± sd at the 4 study sites. Lower-case indicate Tukey test results.

Table 2: Morphological traits plasticity index. Values near 0 indicate similarity in response, while values near 1 indicate a large response. T: tree; C: crown; CTHR: crown/tree height ratio; L: leaf; LMA: leaf mass area; IMPI: intrapopulation morphological plasticity index (± sd in Figure 8).

	LAI	T <sub>height</sub>	C <sub>height</sub>	Trunk	Cover	Volume	C <sub>spheric</sub>	C <sub>asym</sub>	CTHR	L <sub>area</sub>	LMA	IMPI
	0.74	0.80	0.81	0.89	0.96	0.99	0.73	0.38	0.54	0.79	0.54	<b>0.74</b>
Mountain	0.85	0.71	0.65	0.89	0.89	0.96	0.54	0.54	0.42	0.70	0.41	<b>0.69</b>
C <sub>Browsing</sub>	0.63	0.39	0.79	0.83	0.73	0.78	0.83	0.68	0.36	0.60	0.35	<b>0.63</b>
Coastal	0.64	0.33	0.36	0.31	0.54	0.62	0.60	0.22	0.38	0.41	0.60	<b>0.49</b>
Mean	0.72	0.56	0.65	0.73	0.78	0.84	0.67	0.45	0.43	0.63	0.48	

populations turned out to be very plastic, as they both exhibited a high plasticity index (0.74 and 0.69, respectively).

The morphological plasticity index of Coastal population was significantly different from that of North and Mountain, and trees from this population presented the lowest plasticity (0.46). Trees from Coastal Browsing reached a relatively high plasticity figure (0.63), occupying an intermediate position.

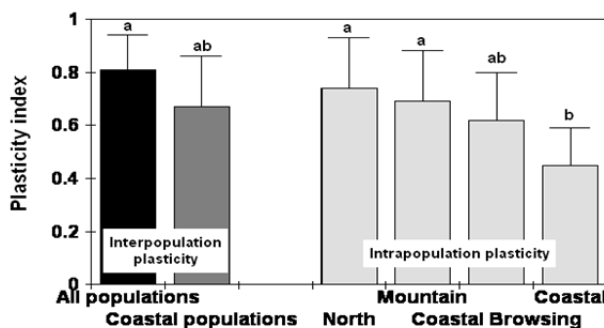


Figure 8: Mean interpopulation and intrapopulation plasticity index of morphological traits of the 4 study populations ± sd. Lower-case indicates post hoc Tukey test results.

When all populations were included to calculate the interpopulation morphological plasticity index, the figure obtained was not different from that of either Mountain or North intra-population plasticities, indicating that these populations contributed the most to the high morphological plasticity found in this species. On the contrary, trees from Coastal were the less plastic.

The studied argan populations showed great morphological differentiation. Trees from the Coastal population presented the greater figures in tree and crown height, crown cover and volume, and LAI. On the contrary, trees from Coastal Browsing, in spite of growing in the same optimum climatic conditions, were the smallest. In this area, the high herbivory brings about a decrease in tree and crown height, cover and canopy volume and LAI. Trees from Coastal Browsing withstand herbivory pressure, not only from goat. Occasionally, migrating herds of dromedaries arrive in the area for browsing the argan trees [17]. It could be suggested that the

small dimensions of trees from this population are due to herbivory pressure.

Argan leaf is small (134 mm<sup>2</sup>). According to Abril and Hanano [18], a reduced size improves the leaf's refrigeration, opposed to the strategy of species with big leaves and thick cuticles, which absorb less radiation. Following their proposal, argan would be a small leaved species, with less production cost, which matches its semideciduous character. The mean LMA of the four populations was 145 g·m<sup>-2</sup>, which means that argan leaves are not especially sclerophyllous. When compared with leaves of other Mediterranean woody species (162 g·m<sup>-2</sup> *Quercus agrifolia* [18]; 142 g·m<sup>-2</sup> *Halimium halimifolium* [19]; 202 g·m<sup>-2</sup> *Rosmarinus officinalis* [20]), it ranks within the semideciduous range, with short lived leaves, whose production is not expensive.

The data obtained in this study suggest that neither LMA nor leaf area were affected by goat browsing. These variables presented the highest values in Coastal and Coastal Browsing populations, although, water deficit is higher in Mountain population and LMA was expected to be higher in this site. Studying in an arid ecosystem of Turkana (Kenya), Oba [21] found significant differences in leaves of *Acacia tortillas* when comparing leaves from grazed and non grazed shoots. Leaves from grazed acacias resulted in bigger LMA than leaves from the protected trees. In the same way, we hypothesized that the grazed trees from Coastal Browsing would have higher LMA than those from Coastal. However, in spite of the fact that Coastal population had been protected from herbivory during the last 18 years, LMA values were similar in both populations, and higher than those of North and Mountain populations.

The smaller crowns and height of trees from the Coastal Browsing population agree with the negative effects of browsing on canopy structure and tree height of woody species described in the literature [22-23]. We expected that under high browsing and human interference, vertical growth should be favoured over lateral growth, as the tree tops are difficult to access for livestock. Subsequently, a higher crown height to width ratio should characterize trees growing in disturbed conditions. We expected the highest C<sub>sphericity</sub> to occur in Coastal Browsing. However, Coastal and Mountain populations showed similar values to those of Coastal Browsing. Differences were only found in the North population, where lateral growth was favoured over vertical growth, and the C<sub>sphericity</sub> index was the lowest.

One of the effects of browsing on woody species is a reduction of crown symmetry. Feedback mechanisms between right and left structures lead to maintained symmetry, which depends on an individual's rate of growth [24]. This effect on C<sub>asymmetry</sub> arises from the difficulty to compensate for growth variations between maximum and minimum diameters [1]. Our results support this theory as C<sub>asymmetry</sub> increased with herbivory pressure in the argan trees. Oppositely, Coastal population trees showed a symmetric structure (low C<sub>asymmetry</sub>). However, herbivory was not the only factor explaining an increase in C<sub>asymmetry</sub>. Climatic conditions also produced a reduction of symmetry, as trees from North and Mountain sites showed higher C<sub>asymmetry</sub> than trees from Coastal. In accord with our results, Alados and El Aich [1] found that an increase in aridity produced an increase in C<sub>asymmetry</sub> of *A. spinosa*, reflecting the sensitivity of this species to aridity, a fact that could explain the values found in the Mountain population.

The ratio of crown/tree height was also affected by human pressure, and was more adverse than weather conditions. Studies on three tree

species [5] describe how this ratio decreased with either decreasing available resources or increasing perturbation, and consequently explain the lower CTHR found in all populations, excepting Coastal.

The plasticity index ecological hypothesis proposes that plants living in similar habitats might have similar plastic responses [25], as plants from more disturbed habitats presumably have higher plasticity than plants from non-disturbed habitats. In our study, the most stressed habitats were considered to be Mountain (because of harsher climatic conditions) and Coastal Browsing (because of high browsing pressure). Coastal was the population with the optimum ecological conditions [12]. Plasticity values found in this study agree with the proposed hypothesis. As expected, Coastal population presented the lowest plasticity and Mountain and North the highest, thus indicating that climatic conditions have a more relevant role in the morphological plasticity of this species than browsing (with intermediate plasticity index). Although Coastal Browsing did not show a different plasticity index from the Coastal population, this population showed a high morphological variability, with the most extreme morphological values with respect to Coastal population.

Considering all the traits together, the patterns of divergence suggest that morphological traits and plasticity indexes are able to

evolve independently. Argan populations showed that under different climatic conditions the prevailing factor playing a significant role is the increase of morphological plasticity, while human influence is the factor seeming to play an important function in the morphological traits.

Many woody species of arid and semiarid ecosystems in Mediterranean shrub, chaparral or African savannas appear to be very resilient to chronic browsing [23, 26]. In our study, browsing and human use of argan trees reduced tree size and leaf production, increasing morphological plasticity. These results could have important implications for argan forest restoration in sites under high human pressure. From a dynamic perspective it can be expected that after a reduction of human interference, the argan stand would reduce inter-tree competition and allow bigger sized trees with higher productive crowns.

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