



## Leaf fluctuating asymmetry of Holm oak in response to drought under contrasting climatic conditions

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Fluctuating asymmetry (FA) can be defined as small, random deviations from bilateral symmetry in structures that, typically, are bilaterally symmetrical. In plants, FA has been used as a tool for monitoring levels of ecological stress. In this work, I analyse the FA response to drought in the Holm oak (*Quercus ilex*) in SE Spain, to test whether FA increases or diminishes when climatic conditions are more stressful. Leaves from three different cohorts, corresponding to one drought year (1995) and two wet years (1996 and 1997) were collected at five sites contrasting in rainfall conditions, from very low to rather high rainfall. In two of the zones, two different morphs of leaves were collected. Furthermore, one of the sites was chosen close to a river, to examine the effect of water enhancement in the trees during drought and post-drought conditions. The results revealed no differences in response to drought in terms of FA between leaf morphs. However, while plants from rainy sites showed a decline in leaf FA from drought to wet years, the water-enhanced site and the dry sites showed scant or negligible differences between years. There was a significant decrease in FA from rainy sites to dry sites. These results suggest that (1) plants living in the more stressful sites are more symmetrical, (2) the more symmetrical plants respond less to yearly variations in drought stress, and (3) the response to yearly variations in drought depend on the climatic conditions in which a tree is living.

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**Keywords:** drought; fluctuating asymmetry; Holm oak, *Quercus ilex*; Mediterranean climate; rainfall

### Introduction

Fluctuating asymmetry (FA) can be defined as small, random deviations from bilateral symmetry in structures that, typically, are bilaterally symmetrical. These deviations may represent developmental perturbations (Palmer & Strobeck, 1986; Parsons, 1990), reflecting interference in the control of developmental processes when growing under given environmental conditions (Møller & Swaddle, 1997). The conditions that are known to increase FA include such environmental factors as temperature,

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nutrients, and light, as well as such genetic factors as mutation, hybridization, and inbreeding (Parsons, 1990; Møller & Swaddle, 1997; Wilsey *et al.*, 1998). Since FA constitutes a quick, simple, and inexpensive measure, it has frequently been used for monitoring levels of ecological stress (Hoffmann & Parsons, 1997; Møller & Swaddle, 1997), either abiotic (pollution: Kozlov *et al.*, 1996; altitude: Wilsey *et al.*, 1998), biotic (competition: Rettig *et al.*, 1997; herbivory: Møller, 1995; Zvereva *et al.*, 1997b, Lempa *et al.*, 2000) or both (Zvereva *et al.*, 1997a).

The use of FA as an index of habitat quality may be especially useful for plant species with wide distributions, which tolerate markedly different conditions throughout their geographical range. However, the main drawback of the use of FA as a diagnostic tool is the difficulty in discriminating the genetic from the environmental components producing FA in the field (Rettig *et al.*, 1997). According to Parsons (1992), relatively severe stress is needed to increase FA under field conditions, since substantial increases in variability occur mainly when stress becomes severe enough to cause injurious changes in a biological system. Therefore, the detection of environmental effects in the field is more reliable under ecologically marginal conditions (Parsons, 1990; Hoffmann & Parsons, 1997). Following this, in an environmental gradient, FA would increase in the same way as the stressful factor, reaching the highest levels at the limit of the distribution gradient (Hoffmann & Parsons, 1997, and references therein). However, adverse environmental conditions may affect the evolutionary process at a range of different levels, and tend to facilitate adaptation to these scenarios; thus, if organisms have had time to adapt to these conditions, and asymmetry reliability reflects the ability of these individuals to cope with current environmental conditions, the more symmetric individuals will be those from the more stressful sites (Møller & Swaddle, 1997).

Mediterranean ecosystems are characterized by contrasting conditions, such as summer drought and winter storms, as well as by sharply variable rainfall between zones and between years (Le Houérou, 1984; Archibold, 1995). How plants cope with different levels of drought stress is of interest, for both purely scientific studies and for economic considerations such as reforestation plans, in which the optimal match of the plant to the environment is needed. In the present work, I use Holm oak (*Quercus ilex*) growing in south-eastern Spain under contrasting rainfall conditions to analyse the effects of drought in the degree of leaf asymmetry shown by trees. The use of naturally established adult trees has the complication of possible genetic differences between populations. However, an experimental approach would be possible only with seedlings, and it is doubtful whether the conclusions reached for an experiment with seedlings–saplings, could be extrapolated to adult trees, since trees of different stages of maturity differ markedly in physiology (Donovan & Ehleringer, 1991). To prevent these problems, I used a repeated-measures sampling protocol, in which plants are their own control (Møller & Swaddle, 1997). I address the following questions: (1) Do different parts within the tree differ in FA response to drought? (2) Are Holm oak leaves prone to higher FA under drought conditions, with variations between years or between sites? (3) Are plant responses to drought stress (yearly variations) modulated by the current climatic conditions in the different places selected (site variations)? The ultimate aim is to determine whether plants living under adverse conditions are either stressed to the limit of survival or adapted to tolerate these conditions.

## Materials and methods

### *Species studied*

The Holm oak, *Quercus ilex*, is a widely distributed species throughout the Mediterranean basin (Archibold, 1995). In Spain, Holm oak woodlands cover around

$2.9 \times 10^6$  ha (Montoya, 1993), and are distributed over a wide range of environmental conditions, from sea level to 2100 m a.s.l., and from semi-arid zones to rather wet areas (350–1200 mm of annual rainfall, Franco, 1990; Montoya, 1993; see also Castro-Díez *et al.*, 1997). This is a slow-growing, long-lived tree (up to 600 years), reach 25 m in height, and is quite resistant to herbivory and losses of limbs or trunk by breakage, cutting or fire, by resprouting from a powerful root system. The reproductive system is similar to that of other *Quercus* species, pollination (in spring) is anemophilous and the seeds (acorns, produced in autumn–early winter) are dispersed mainly by jays (*Garrulus glandarius*) and rodents. While seed dispersal is quite effective and reaches long distances (up to 1000 m, Gómez *et al.*, in press), there is no accurate information about pollination distances, although Montoya (1993) indicate problems of inbreeding depression by self-pollination when natural woodlands are cleared in *dehesas*. Holm oak leaves are highly variable in shape, and leaf morphology is more directly influenced by rainfall than in other *Quercus* species (Castro-Díez *et al.*, 1997). Holm oak usually has two distinct leaf morphs: one typical of the canopy, in adult trees (hereafter ‘canopy’); and the other typical of the shoots in juvenile trees, these being much more spiny and sclerophyllous (Franco, 1990). Both types of leaves, however, may coincide in the same individual, since adult trees sometimes produce shoots from the trunk (hereafter ‘sprouts’).

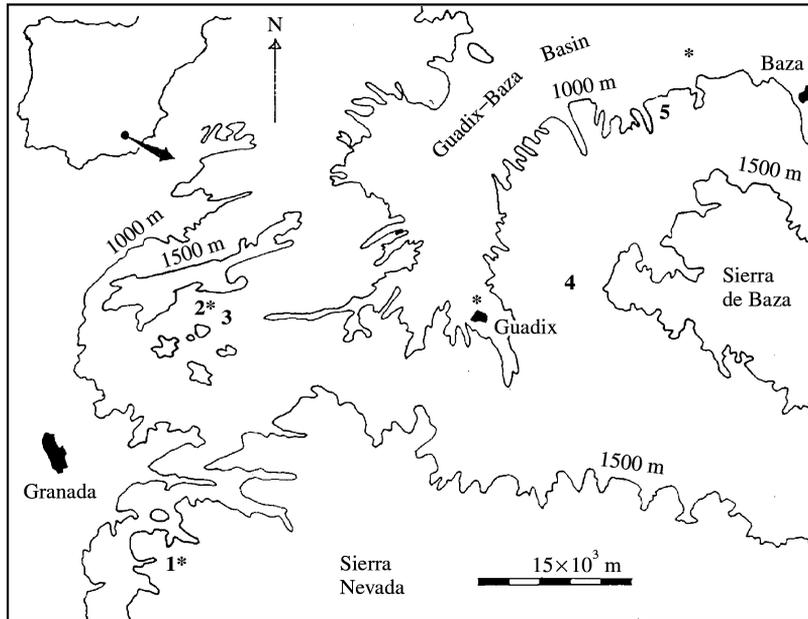
#### *Study sites and climatic conditions*

Five sites, hereafter Cortijuela, Molinillo, Fardes, Ladihonda and Fazares, were selected as sampling areas (Fig. 1). Sites were chosen in a curved line SW–NE representing a strong rainfall gradient, from mid-altitude mountains towards an arid basin. Soil is calcic regosol in the five sites studied. Molinillo, Ladihonda and Fazares, are *dehesa*-like woodlands, with some human management (mainly sheep raising) and low tree density (10–30 oaks ha<sup>-1</sup>), while Cortijuela is an abandoned cultivated area in which adult-tree density is 50 oaks ha<sup>-1</sup>, and only Fardes is a natural, dense woodland. The two farthest sites are 70 km apart. All the trees sampled, according to Franco (1990), belong to the subspecies *Quercus ilex ballota*.

Yearly variation in rainfall was considered in combination with spatial variation described above. Southern Spain suffered a long and heavy drought in recent years: for instance, the city of Granada (see Fig. 1), with an average rainfall of 382 mm during the period 1961–1990, reached only 262 mm on average in the period 1991–1995, and only 174 mm in the period October 1994–September 1995 (Junta de Andalucía, 1996). The drought suddenly ended in November 1995, with rainfall exceeding 700 mm in 1996 and 1997. This does mean that the area in which study sites are included received in 1995 a 50–70% of the historical rainfall average, while in 1996 and 1997 it received 170–180% (Junta de Andalucía, 1996, 1997a, 1998). Although well adapted to the dry Mediterranean climate, the Holm oak suffered severe defoliation and even mortality during this drought period (Junta de Andalucía, 1996). Since Holm oak leaves remain on the tree for several years (Franco, 1990), and the yearly growth scars of the shoots are easily recognizable, leaves can reliably be assigned to different cohorts with different climatic conditions.

#### *Sampling design*

At each of the five selected sites, I chose 10 trees in an area of *ca.* 1 ha, and haphazardly chose four-five shoots, equally distributed over the canopy circumference, collecting 15–25 leaves from each year (1995, drought year, and 1996 and 1997, rainy years) and level (canopy and sprouts). I collected canopy leaves from twigs growing at over 2 m in height. Leaves were collected from sprouts only in Cortijuela



**Figure 1.** Location of the study sites. Sites are 1: Cortijuela (816 mm rainfall), 2: Molinillo (838), 3: Fardes (838), 4: Ladihonda (300), and 5: Fazares (337). Rainfall data are from the nearest climatic station available (asterisks in the map, averages for series of 20–30 years, taken from Junta de Andalucía, 1997*b*), except for Cortijuela, from a climatic station at the site which includes only a 10-year series (1991–2000).

and Fazares; this was not possible either in Molinillo and Ladihonda, because the sprouts of these trees had been pruned off; in Fardes, the sprouts, though present, were too scarce to allow an adequate sampling. In Fardes, trees <5 m from a riverbank were selected, to ensure higher water availability.

In the laboratory, leaves were dried between sheets of filter paper. Before measuring, I removed all folded or damaged leaves, and from the remaining ones, I randomly took 10 leaves per tree, year, level, and site, for a total of 2100 leaves. Measurements made on the leaves were maximum width of the left (WL) and right (WR) sides of the leaf, from the midrib to the outer leaf margin, without considering spines.

#### *Data analysis*

To test the accuracy of the measurements, I remeasured 70 randomly collected leaves (one leaf per tree and level), and compared the new measurements of WR and WL. Because measurement error can confound estimates of FA, symmetry differences measured must be larger than the measurement error. The range in absolute bilateral differences for the 70 remeasured leaves proved to be 0–2.12 mm ( $0.63 \pm 0.05$  mm, mean  $\pm$  S.E.), while the maximum absolute difference between the original and the repeated measures was 0.32 mm for WR ( $0.10 \pm 0.01$  mm) and 0.23 for WL ( $0.09 \pm 0.01$  mm). Furthermore, a Pearson correlation between original and repeated measurements offered  $r^2$  values of 0.996 for WR and 0.998 for WL, thus I considered my measurements reliable.

Before the statistical analysis, I checked whether the kind of bilateral asymmetry found in the leaves of the Holm oak could be considered true FA (Palmer & Strobeck,

1986). The check was made separately for each site, level, and year (see Appendix A). To check for antisymmetry (significant differences on the WL–WR distribution from the normal curve), the WL–WR values were tested to fit the normal curve. There were no significant differences from normality (invariably  $p > 0.078$ , Shapiro–Wilk test). Absence of directional asymmetry (significant differences in size between leaf sides) was checked by testing that the average WL–WR value did not differ from zero (invariably  $p > 0.05$ , Student's *t*-test). On the other hand, absolute value of WR–WL significantly and positively correlated (Pearson *r*) with leaf width except in one case (Ladikhonda year 1997). For this reason, I used the expression  $FA = 2|WL - WR| / (WL + WR)$  as the FA index, to correct for leaf size (Palmer & Strobeck, 1986; Møller & Swaddle, 1997).

The factors considered in the statistical analyses were site (the five sampling localities), level (canopy and sprouts), year, and individual; all the interactions were also examined. Data were analysed with a nested, multivariate repeated-measures analysis of variance (MANOVA, von Ende, 1993), a procedure that allows individuals to serve as their own controls under different conditions. MANOVA was preferred instead of univariate RMANOVA because data severely departed from the assumption of sphericity (SAS Institute Inc., 1989). Analysis was performed with the PROC GLM of SAS statistical package (SAS Institute Inc., 1989). Two different models were tested: in the first, only leaves from the canopy were used, with the five sampling sites included, site and individual (nested in site) being between-subject factors, and year within-subject. The second model used leaves from both the canopy and sprouts, and included only Cortijuela and Fazares as a zone. In this model, the site, level and individual (nested in site) were the between-subject factors, and year within-subject. In both models, the dependent variable was FA.

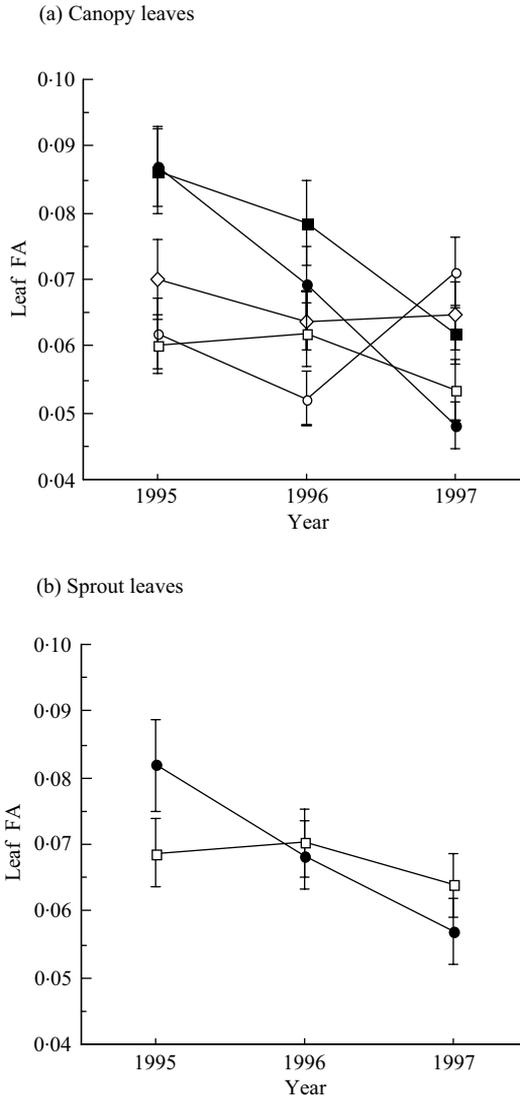
## Results

### *FA in canopy leaves*

The amount of FA in canopy leaves varied widely both between years and between sites, and the effect of the yearly variations differed between sites (Fig. 2, Table 1). Furthermore, although there were no differences between individuals, the interaction with year shows that the responses of individual trees differed between years (Fig. 2, Table 1). The FA response followed the same pattern in Cortijuela and Molinillo, and was similar to that in Fardes, with diminishing FA levels from 1995 to 1997, although the pattern was less clear in Fardes, with scant differences between years. However, there was no clear response either in Ladikhonda or in Fazares, where the highest FA levels were recorded in 1997 and 1996, respectively (Fig. 2). Furthermore, Cortijuela, Molinillo and Fardes registered higher levels of FA than Ladikhonda and Fazares (Fig. 2(a), Table 1).

### *FA in canopy vs. sprout leaves*

The amount of FA both in canopy and in sprout leaves again varied between years; however, no differences between sites were found, and only the effect of the yearly variations differed between sites and individuals within sites (Fig. 2, Table 2). Similarly, no differences appeared between levels, individuals, and their interactions, unless yearly variation is considered: the different levels of different individuals varied in response to yearly variations. While in Cortijuela the FA diminished both in canopy and sprouts from 1995 to 1997, in Fazares the response was equivocal, with higher



**Figure 2.** Fluctuating asymmetry values in (a) the canopy leaves for the five sites: (—●—), Cortijuela; (—■—), Molinillo, (—◇—), Fardes; (—○—), Ladihonda; (—□—), Fazares; and (b) the sprout leaves: (—●—), Cortijuela; (—□—), Fazares; for Cortijuela and Fazares, examined in the 3 years of study. Each point represents mean and standard error for 100 leaves (10 leaves by 10 individuals).

levels in 1996 and lower in 1995 and 1997. There were no differences in terms of FA between canopy and sprouts (Fig. 2, Table 2).

The results of the analysis, both for canopy and canopy *vs.* sprout leaves, can be summarized as follows: on average, FA in leaves showed no differences between individuals, and between levels within an individual, and only for canopy leaves were there differences between sites; however, differences between years were found, and these variations varied between sites, between individuals within sites, and between levels within individuals.

**Table 1.** Summary of the nested, multivariate repeated-measures analysis of variance for leaf FA in canopy leaves

Source of variation	df. Num	df. Den	$\lambda$	$F$	$p$
Site	4	450	0.9535	5.49	0.0003
Ind(Site)	45	450	0.8984	1.13	0.2661
Year	2	449	0.9671	7.64	0.0005
Year*Site	8	898	0.9289	4.22	0.0001
Year*Ind(Site)	90	898	0.7557	1.50	0.0027

Note: df. represents the degrees of freedom (Num, numerator and Den, denominator);  $\lambda$  is the Wilks' lambda;  $F$  is the  $F$ -ratio value of each effect and  $p$  is the significance level. Ind means individual.

## Discussion

The comparison between canopy and sprouts of Holm oak showed that, despite the pattern differences between sites, specimens from both Cortijuera and Fazares showed rather similar FA patterns at both levels. That is, although sprout leaves were more sclerophyllous and hence might be more appropriate to drought conditions, this does not necessarily imply a difference in terms of FA. Cowart & Graham (1999) found in the fig (*Ficus carica*) differences in FA depending of the height and position of leaves in the crown of the tree, explaining these variations by differences in temperature and light intensity. In a similar way, Roy & Stanton (1999) showed in wild mustard (*Sinapis arvensis*) that asymmetry varies among organs within individuals under a given environmental stress. The data offered here suggest that in Holm oak the plant as a whole responds to drought stress, and there are no plant parts less prone to FA than others.

By contrast, there were substantial differences in FA in canopy leaves between zones and between years. In the two wettest of the five sites studied, Cortijuera and Molinillo, high levels of FA appeared during drought, with progressively lower levels of leaf FA as rainfall increased. Furthermore, enhanced water availability at the Fardes site reduced the FA values in comparison with the Molinillo site, only 3 km away but without an extra water supply. However, in Ladihonda and Fazares, the driest sites, canopy leaves showed scant FA variation from year to year, and Ladihonda in fact

**Table 2.** Summary of the nested, multivariate repeated-measures analysis of variance for leaf FA in canopy vs. sprout leaves, for the sites Cortijuera and Fazares

Source of variation	df. Num	df. Den	$\lambda$	$f$	$P$
Site	1	360	0.9898	3.69	0.0555
Level	1	360	0.9916	3.06	0.0809
Site*Level	1	360	0.9945	1.97	0.1609
Ind(Site)	18	360	0.9505	1.04	0.4111
Level*Ind(Site)	18	360	0.9543	0.96	0.5084
Year	2	359	0.9251	14.52	0.0001
Year*Site	2	359	0.9652	6.47	0.0017
Year*Level	2	359	0.9962	0.69	0.5043
Year*Site*Level	2	359	0.9978	0.39	0.6758
Year*Ind(Site)	36	718	0.8686	1.45	0.0432
Year*Level*Ind(Site)	36	718	0.8637	1.52	0.0283

Note: df. represents the degrees of freedom (Num, numerator and Den, denominator);  $\lambda$  is the Wilks' lambda;  $F$  is the  $F$ -ratio value of each effect and  $p$  is the significance level. Ind means individual.

increased in FA from 1996 to 1997. Both the FA changes in Cortijuela and Molinillo, as well as the lack of change in Fardes, the wetter site, suggest that drought is a major factor determining leaf FA in the Holm oak. If detection of FA due to environmental stress in the field is more reliable under marginal conditions (Parsons, 1990; Hoffmann & Parsons, 1997), the overall pattern for the sites studied would reflect higher levels and wider between-year variations of FA in the drier sites, Ladihonda and Fazares, and lower levels and narrower variations in the wet sites, Cortijuela, Molinillo and Fardes. However, the pattern found was the reverse.

There are two alternative hypotheses to explain the results found here. The first is that there has been a genetic fitting to these adverse environmental conditions (Møller & Swaddle, 1997)—that is, plants from drier sites perform better against stressful situations because they are adapted to these conditions. Adaptation can explain both the tendency towards decreased FA from wettest to driest sites, and the lack of response in driest sites to yearly variations in rainfall; the more symmetric plants from dry sites were more tolerant to stress, either yearly variation or sustained low rainfall, than were the more asymmetric ones from wet sites (see e.g. Hoffmann & Parsons, 1993). In fact, Hoffmann & Parsons (1993) suggest that these stressful conditions can lead to rapid evolutionary change by causing intense natural selection. In this sense, several traits related with the ability of Holm oak saplings to tolerate drought, as for instance root:shoot ratio and leaf area, are genetically fixed in Holm oak (Leiva & Fernández-Alés, 1998). A noteworthy possibility has been suggested by Hochwender & Fritz (1999) and Martel *et al.* (1999), who found in *Salix* and *Betula*, respectively, increased FA under optimal growth conditions, because the speed of the leaf growth is very quick and this triggers developmental instability. This could be the case in Ladihonda, where FA sharply rose in 1997, when the growing conditions were optimal for trees. However, the other four sites either maintained or diminished their FA values when conditions improved.

The second hypothesis is that plants have simply become accustomed to stress. A plastic accommodation to stress would make old plants more symmetrical because asymmetry tends to decline over the lifetime of the plant (Roy & Stanton, 1999). However, this possibility does not explain the lack of significant response in Ladihonda and Fazares during the wet years. Results show that stressed plants registered lower FA levels in two years of reduced drought stress (Cortijuela and Molinillo sites), but we have no data concerning the time required for plants accustomed to stress to respond to a new non-stressful situation. If the response is as quick as for non-stressful sites, the evidence would favour the hypothesis of local adaptation.

The possibility of local adaptation of plants to stressful sites might suggest the use of FA as a good diagnosis character to assess the stress tolerance of a tree variety, line, or individual: leaf FA would be considered as a 'quality index' revealing the plant capacity to tolerate drought stress (Hoffmann & Parsons, 1997). If drought tolerance is heritable and well measurable by FA, it would be easy to select mother trees with low FA levels to ensure saplings with high tolerance to drought. However, Roy & Stanton (1999) showed in wild mustard that, although experimental plants subjected to different stressful treatments increased in terms of FA with respect to control plants, the correlation between individual fitness and asymmetry was not strong, indicating that FA cannot be used to select suboptimal individuals from a population during selection, at least in the current state of knowledge. Furthermore, the results presented here also show that Holm oak trees experience different levels of drought stress depending on the climatic conditions in which a tree is living. This can mask the tree's response when different populations are analysed, but the problem may be avoided by using a repeated-measures procedure, in which individuals are their own controls under different climatic conditions (Møller & Swaddle, 1997).

In conclusion, in Holm oak (1) the FA of different leaf morphs does not differ in response to drought, (2) leaves are prone to higher FA when live in non-stressful sites and are subjected to stressful drought conditions, and (3) the response to yearly drought variations depends on the climatic conditions in which a tree is living. In short, plants living in the more stressful sites are more symmetrical.

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## Appendix A

Summary of descriptive data for the sites, levels, and years studied is given in Table A1. WL + WR represents leaf size (in mm), WL–WR represents individual leaf asymmetry,  $|WL - WR|$  is the absolute value of leaf asymmetry, *Diff to 0* represents the *t* values (Student's *t*-test) and its *p* associated, *Normality* are the *W* values of the Shapiro–Wilk test for normality and its *p* associated, *Slope* is the slope of the regression of  $|WL - WR|$  vs. leaf size, and FA are values of fluctuating asymmetry  $FA = 2|WL - WR|/(WL + WR)$ . Skewness and kurtosis are also indicated. Means are always followed by  $\pm 1$  S.E. Sample size is 10 trees with 10 leaves each in every row.

Table A1

Site	Year	WL + WR	WL-WR	WL-WR	Diff to 0	Normality	Skew	Kurt	Slope	FA
Cortijuela canopy	1995	13.86 ± 0.40	0.035 ± 0.076	0.599 ± 0.047	0.459/0.647	0.979/0.490	-0.366	0.184	0.045 ± 0.011	0.086 ± 0.006
	1996	14.83 ± 0.33	-0.058 ± 0.076	0.528 ± 0.049	-0.807/0.422	0.967/0.078	-0.619	2.695	0.058 ± 0.014	0.069 ± 0.006
	1997	17.38 ± 0.35	0.056 ± 0.052	0.418 ± 0.032	1.075/0.285	0.978/0.435	0.361	-0.132	0.023 ± 0.009	0.048 ± 0.004
Cortijuela sprouts	1995	14.30 ± 0.38	-0.007 ± 0.061	0.583 ± 0.056	-0.080/0.936	0.965/0.062	0.564	4.484	0.037 ± 0.014	0.083 ± 0.007
	1996	18.59 ± 0.45	-0.060 ± 0.081	0.642 ± 0.051	-0.733/0.465	0.981/0.561	-0.047	-0.103	0.039 ± 0.011	0.068 ± 0.005
	1997	18.82 ± 0.35	0.143 ± 0.082	0.538 ± 0.050	1.979/0.051	0.972/0.183	0.477	1.454	0.033 ± 0.014	0.057 ± 0.005
Molinillo canopy	1995	14.71 ± 0.31	0.073 ± 0.073	0.636 ± 0.049	0.915/0.362	0.988/0.909	0.181	0.291	0.043 ± 0.015	0.087 ± 0.006
	1996	18.04 ± 0.57	-0.115 ± 0.080	0.719 ± 0.062	-1.220/0.226	0.988/0.910	0.286	1.643	0.043 ± 0.010	0.079 ± 0.006
	1997	14.10 ± 0.32	0.036 ± 0.094	0.442 ± 0.036	0.627/0.532	0.988/0.894	-0.422	0.693	0.040 ± 0.011	0.062 ± 0.005
Fardes canopy	1995	12.10 ± 0.22	-0.028 ± 0.057	0.416 ± 0.036	-0.523/0.602	0.981/0.586	0.209	0.965	0.033 ± 0.016	0.068 ± 0.005
	1996	13.77 ± 0.27	0.048 ± 0.054	0.439 ± 0.032	0.893/0.374	0.984/0.742	0.033	-0.283	0.028 ± 0.012	0.064 ± 0.004
	1997	13.94 ± 0.22	-0.069 ± 0.057	0.451 ± 0.035	-1.204/0.231	0.990/0.948	-0.143	0.078	0.032 ± 0.015	0.065 ± 0.005
Ladihonda canopy	1995	12.79 ± 0.30	-0.075 ± 0.054	0.400 ± 0.037	-1.400/0.165	0.985/0.765	0.165	2.356	0.039 ± 0.012	0.062 ± 0.005
	1996	15.35 ± 0.22	-0.082 ± 0.050	0.403 ± 0.032	-1.605/0.112	0.978/0.446	-0.098	-0.060	0.033 ± 0.014	0.052 ± 0.004
	1997	14.82 ± 0.27	0.058 ± 0.063	0.502 ± 0.039	1.072/0.285	0.977/0.401	0.295	0.348	0.008 ± 0.014	0.070 ± 0.005
Fazares canopy	1995	14.09 ± 0.30	0.075 ± 0.052	0.421 ± 0.032	1.424/0.158	0.982/0.643	-0.127	0.054	0.027 ± 0.010	0.060 ± 0.004
	1996	15.13 ± 0.29	-0.069 ± 0.059	0.464 ± 0.036	-1.179/0.241	0.989/0.923	0.164	0.621	0.024 ± 0.012	0.062 ± 0.005
	1997	13.64 ± 0.23	0.076 ± 0.050	0.371 ± 0.034	1.527/0.130	0.987/0.852	0.073	0.822	0.047 ± 0.014	0.054 ± 0.005
Fazares sprouts	1995	17.30 ± 0.32	-0.048 ± 0.077	0.604 ± 0.048	-0.630/0.530	0.989/0.935	0.089	0.273	0.050 ± 0.014	0.069 ± 0.005
	1996	23.92 ± 0.48	-0.006 ± 0.106	0.837 ± 0.064	-0.056/0.955	0.979/0.465	-0.450	0.716	0.035 ± 0.013	0.070 ± 0.005
	1997	19.52 ± 0.40	-0.059 ± 0.085	0.642 ± 0.056	-0.685/0.498	0.978/0.436	0.244	2.357	0.060 ± 0.013	0.064 ± 0.005