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GENDER-RELATED DEVELOPMENTAL INSTABILITY AND HERBIVORY OF *PISTACIA ATLANTICA* ACROSS A STEEP ENVIRONMENTAL GRADIENT

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Abstract: To examine gender-related developmental instability and herbivory of a plant across a steep climatic gradient, we studied *Pistacia atlantica* DESF., a dioecious tree of the Irano-Turanian zone in the Middle East. Leaves were sampled from five populations along a climatic gradient in Israel from mesic Mediterranean to xeric (and geographically peripheral) sites. Leaves of the xeric populations were ca. 25% smaller in size (length) than leaves of other populations. Leaf developmental instability (an indicator of stress) was examined using the measurement of leaf asymmetry (LA), estimated by the deviation from the origin of paired lateral leaflets and by the presence vs. absence of the terminal leaflet. LA was not correlated with the climatic (site) gradient and had the highest, though not significantly, levels in the intermediate ecotonal zone between the Mediterranean and the arid ecosystems. Male trees were 13% higher in LA than females. Density of two specialist gall-forming aphids varied with site but was not affected by plant gender. Gender-related developmental instability is discussed in relation to resource allocation in early spring. Because the study was limited to five populations further research is clearly needed.

Keywords: Aphids, Environmental stress, Fordinae, Gall, Gender, Leaf asymmetry, Peripheral populations

INTRODUCTION

A comparative study of populations across sharp environmental gradients provides us with an opportunity to examine ecological and evolutionary patterns within species' distribution ranges. *Pistacia atlantica* DESF. (*Anacardiaceae*) is a deciduous dioecious tree with unbiased sex ratios (BOGEN et al. 1997, ROTTENBERG 1998). The tree is wind pollinated and males' budbursts generally follow those of female flowers (protandry). *P. atlantica* has a typical Irano-Turanian distribution range, from Central Asia through the Middle East to North Africa (ZOHARY 1952). In Israel *P. atlantica* is distributed discontinuously from the Golan Heights through the Galilee to the Negev highlands (ZOHARY 1952). This wide distribution along diverse climatic regions exposes local populations to different growing conditions. For example, in north and central Israel plants may receive over 600 mm mean annual precipitation whereas in the Negev they get nearly 100 mm precipitation annually. Thus, trees in the Negev comprise geographically and ecologically peripheral populations apparently exposed to harsher environmental conditions and limited resources. It has been shown that leaf morphology, physiology and chemistry of two related species *P. lentiscus* and *P. terebinthus* vary with climatic conditions (e.g. CASTRO-DÍEZ et al. 1998).

Fig. 1. Location of the study sites in Israel from the Hula Valley (Ein Avazim) in the north to Wadi Lotz in the Negev Highlands.

In the Pleistocene, when climatic conditions were cooler and more mesic, *P. atlantica* was more continuously distributed (DANIN 1999). In the Holocene the climate became warmer and drier, leaving *P. atlantica* populations as relict patches in the higher and cooler areas in the dry regions (e.g., the Negev Highlands and Sinai Peninsula). Most other populations in what are today arid regions have become extinct (DANIN 1999). While the general long-term trend is one of decreasing populations, a central question that arises is whether those remaining are under stress. These relict populations seem to have been viable, indicating that they may have adapted to marginal conditions.

An important approach for examining the response of individuals to their environmental conditions is by estimating developmental instability. Various indicators of developmental instability have been suggested (LEARY & ALLENDORF 1989). These reflect an organism's ability to accomplish normal development of repeated traits in the face of environmental and genetic stress (GRAHAM et al. 1993). Genetic stress may include the loss of genetic diversity due to inbreeding and genetic drift, as well as disruption of co-adapted gene complexes (CLARKE 1995, MØLLER & SWADDLE 1997). Measurements that have been proposed include fluctuating asymmetry between the two sides of a bilaterally symmetrical trait (e.g., wing, leaf area), as well as fractal dimensions in animals and plants and phyllotaxy (the arrangement of leaves on the stem) in plants (GRAHAM et al. 1993). Environmental stresses, such as water and nutrient deficiency, high salinity and shade, have been shown to increase plant developmental instability (ROY & STANTON 1999), which may therefore serve as a potential tool for evaluating the individuals' responses to environmental gradients (KARK 2001, KARK et al. 2001).

Insect herbivores may be affected directly by the environmental gradient, or indirectly via host plant quality, although the nature of their response is species-specific and highly variable (e.g., BOECKLEN & HOFFMAN 1993, INBAR et al. 2001). Leaf size (as an indicator of plant vigor) may be associated with higher herbivore densities, especially of gall-formers and leaf-miners that have established intimate relationships with their host plants (PRICE 1991).

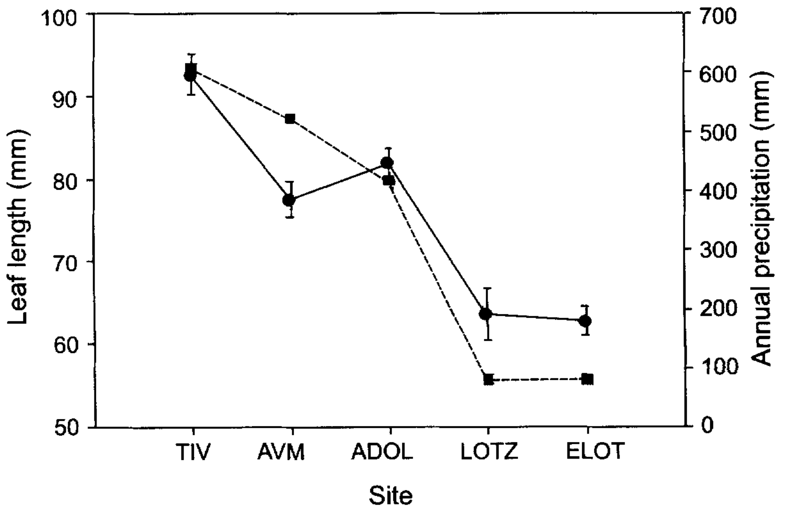

Fig. 2. The association between mean (± SE) *P. atlantica* leaf length (circles) and mean annual precipitation (squares) in the study sites (Spearman's $r = 0.87$, $P = 0.05$). TIV – Tivon; AVM – Ein Avazim; ADOL – Adolam; ELOT – Wadi Elot; LOTZ – Wadi Lotz. Sites are arranged from highest (left) to lowest (right) rainfall.

The relationship between host asymmetry and herbivory varies among systems. It is questionable whether the herbivores interact directly or indirectly with host plant developmental instability (MØLLER 1995, WIGGINS 1997). LEMPA et al. (2000) argued that such relationships may depend on the linkage between the factors inducing asymmetry and biochemical pathways. They suggested that if asymmetry is associated with the production of defensive compounds the outcome will be reduced herbivory.

Here we focused on the association between climatic conditions and *P. atlantica* leaf traits. We asked how this association may affect density of specialist herbivores: gall-forming aphids (see Methods); these insects entirely depend on the quality of their host plant. Specifically, we addressed the following questions:

(1) Do *P. atlantica* leaf size and developmental instability (leaf asymmetry) change along the climatic gradient?

(2) Do differential growing conditions of the tree affect the density of two host-specific insect herbivores? Is there a correlation between the level of herbivory and host developmental instability?

(3) As male and female individuals of *Pistacia* and other dioecious plants may differ in many phenological, morphological and biochemical aspects (JONASSON et al. 1997, DAWSON & GEBER 1999, CORREIA & DIAZ BARRADAS 2000), how are the foregoing questions related to plant gender?

MATERIAL AND METHODS

Study sites

We examined five *P. atlantica* populations across a steep climatic gradient in Israel, from mesic Mediterranean (north) to arid periphery (south) (Fig. 1). The populations were Ein

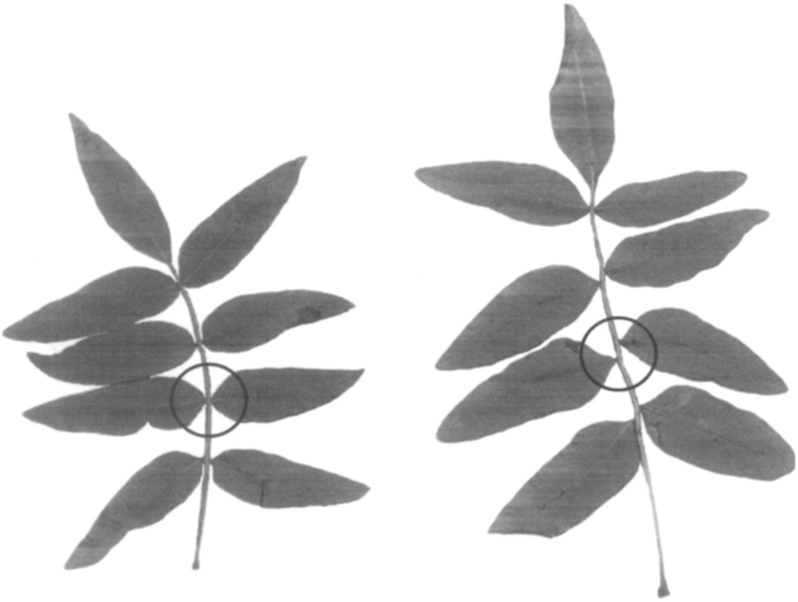

Fig. 3. Symmetric (left) and asymmetric (right) *P. atlantica* leaves. The indication for asymmetry (developmental instability) was based on the distance between the origins of parallel leaflets along the petiole (see circles). Here both leaves have a terminal leaflet.

Avazim (AVM) in the Hula valley of northern Israel ($n = 20$ trees); Tivon (TIV) in the lower Galilee below Mt. Carmel ($n = 20$), Adolam (ADOL) in the foothills of southern Judean mountains ($n = 16$); Wadi Elot (ELOT) in the Negev desert highlands ($n = 25$); and Wadi Lotz (LOTZ) 10 km north of ELOT with similar climatic conditions ($n = 15$ trees). LOTZ and ELOT are located in the Negev desert highlands, the edge of the species global range (Fig. 2). AVM and TIV populations are composed of hundreds of trees, LOTZ and ELOT have about a hundred trees, and the ADOL has only a few dozen.

The aphids

The two gall-forming aphids (Homoptera, Pemphigidae) were examined in this study; *Smynthurodes betae* (WEST.) and *Slavum wertheimae* HRL both form galls specifically on *P. atlantica*. The basic biology of this aphid has been studied extensively (INBAR & WOOL 1995, INBAR et al. 2004, WERTHEIM & LINDER 1961, WOOL & BOGEN 1999, WOOL & BURSTEIN 1991). The first (temporary) galls of *S. betae* are formed early in the spring on the leaflet midrib by fundatrices hatching from overwintering eggs. Within each gall several second generations are produced parthenogenetically. They soon leave the temporary galls and produce the "final", spindle-shaped gall on the leaflet margin. In the fall winged aphids leave the galls and the next generations develop on the roots of non-specific (secondary) hosts. In the following spring winged aphids (sexuparae) return to *P. atlantica* and produce males and females. After mating the fertilized eggs undergo diapause on the tree, and fundatrices hatch from them one year later. Here, we examined the density of the final

Table 1. Two-Way ANOVA table summarizing the effect of host plant gender and geographical sites on plant traits and density of galling aphids.

	d.f. effect	d.f. error	*F*	*P*
Leaf Asymmetry				
Site	4	86	1.6	0.18
Gender	1	86	3.86	0.05
Site × Gender	4	86	0.71	0.53
Terminal leaflet				
Site	4	86	1.63	0.17
Gender	1	86	0.001	0.95
Site × Gender	4	86	0.67	0.60
Leaf length				
Site	4	86	30.55	< 0.01
Gender	1	86	0.10	0.74
Site × Gender	4	86	0.35	0.84
Smynthurodes betae				
Site	4	86	9.06	< 0.01
Gender	1	86	1.69	0.19
Site × Gender	4	86	3.11	0.02
Slavum wertheimae				
Site	4	86	10.85	< 0.01
Gender	1	86	0.37	0.54
Site × Gender	4	86	0.71	0.58

(spindle-shaped) galls. *S. wertheimae* galls have a similar life cycle with some modifications. Only one cauliflower-shaped gall is produced on the lateral buds; the sexuparae are produced within the galls so they have an annual cycle without secondary hosts.

Sampling

Sampling was conducted in July–August on mature trees (ca. 4 m height × 4 m wide). From each tree we randomly collected 12 leaves from the middle of the shoot. The leaves were taped on a plant press and were allowed to dry before analyses. We counted the total number of cauliflower galls on each tree. Smaller spindle-shaped galls were counted on six randomly selected shoots.

Measurements

Measurements were taken by the same person with a digital caliper on photocopied leaves. Leaf length was measured along the petiole. We used two indicators to estimate developmental instability: first, mean leaf asymmetry (LA) in the origin of the paired lateral leaflets was measured (Fig. 3, see also FREEMAN et al. 1993, MØLLER 1998). Mean LA was divided by leaf length for standardization. Second, we used the ratio of presence to absence of the terminal leaflet as an indicator of developmental instability. Usually *P. atlantica* has imparipinnate leaves, i.e. with a terminal leaflet (ZOHARY 1952; see also AUSLANDER et al.

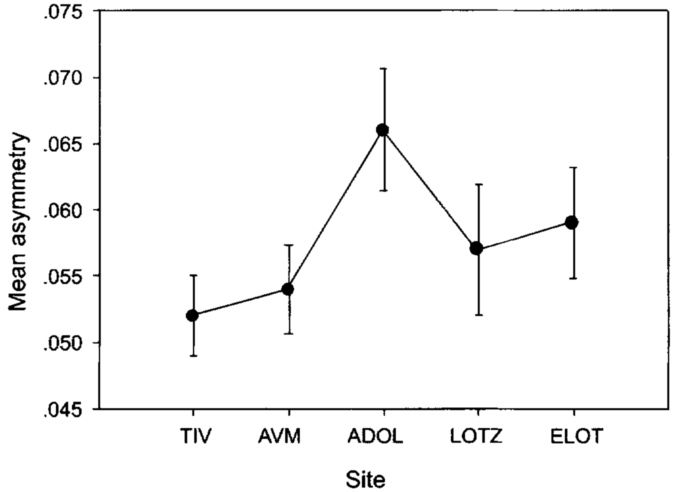

Fig. 4. Mean (±SE) leaf asymmetry in *P. atlantica* pinnate leaves. Asymmetry was calculated by the mean deviation of the origin of the paired parallel leaflets in each leaf (see methods). The X-axis was arranged along a rainfall gradient. Population codes as in Fig. 2.

1998). This may be a useful indicator of developmental instability (GRAHAM et al. 1993). Mean percentage of leaves without a terminal leaflet per tree was calculated. Repeatability (r) was calculated as the intra-class correlation coefficient on the basis of a variance component derived from a one way ANOVA of repeated measurements (LESSELLS & BOAG 1987) of one leaf from each tree. The analysis showed high repeatability of LA measurement, $r = 0.96$, ($F_{95\text{-}191} = 44.3$, $P << 0.01$). The data were analyzed using Two-Way ANOVA with site and plant gender as main effects. We used Analysis of Covariance (ANCOVA), with leaf length as the covariate, to examine the possible effect of plant gender on gall density. Data on LA and percentage of leaves with missing terminal leaflet were normalized with log and arcsine transformed before analysis. All statistical analyses were performed with Statistica software (StatSoft Inc. Tulsa, OK, USA).

RESULTS

Geographical trends

Mean leaf length in peripheral populations (LOTZ and ELOT) is nearly 25% lower ($P < 0.01$) than in central and northern Israel (Fig. 2; Table 1). Although the mean LA (Fig. 4) is a bit higher in central and southern Israel the differences are not statistically significant (Table 1). Overall, the terminal leaflet is missing in 13.8% (± 0.01 SE) of the leaves and there is no significant correlation between the location of a population along the geographical gradient and this estimate (Table 1). LA is not correlated with the absence of terminal leaflet (Table 2). Density of the cauliflower and spindle-shape galls varies with the site (Fig. 5; Table 1). The cauliflower galls are absent from ADOL and reach remarkably high densities in the southern Negev highlands. Spindle-shaped galls, however, are relatively rare in the Negev (ADOL and LOTZ) and in AVM but very dense in ADOL and TIV (Fig. 5). Leaf size is negatively correlated with the density of cauliflower galls but positively correlated with the

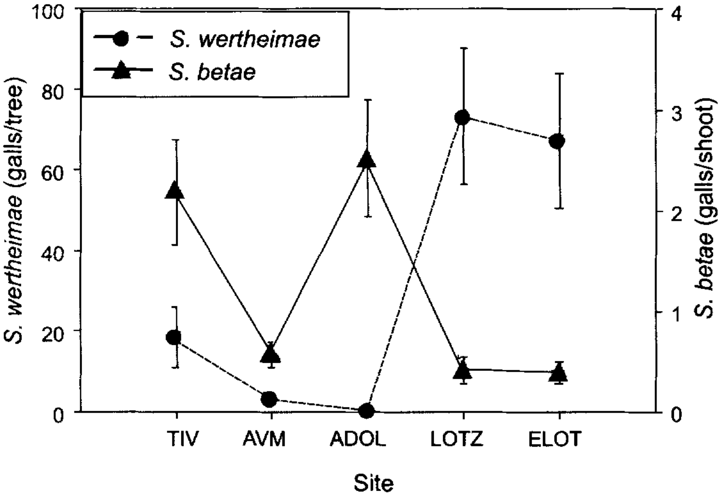

Fig. 5. The mean (± SE) density of the gall-forming aphids on *P. atlantica*. *S. wertheimae* density is the mean number of galls/tree. *S. betae* density is the mean number of galls/shoot/tree. The X-axis was arranged along a rainfall gradient as in Fig. 2. Population codes as in Fig. 2.

density of the spindle-shaped galls. Neither gall-former density is correlated with LA or the rate of missing terminal leaflets (Table 2).

Gender-related trends

In contrast to the absence of site effect, LA is significantly affected by plant gender. Male LA (0.64 ± 0.027) is 13% higher than that of female leaves (0.54 ± 0.023, Table 1). In all populations, 13% of male and 14.2% of female *P. atlantica* leaves lack terminal leaflets ($t = 0.39$, d.f. = 94, n.s.). Mean male leaf length is 7.75 ± 0.22 cm longer (although not significantly) than mean female leaf length (7.32 ± 0.2 cm). Gall density is not significantly related to host gender in either aphid species. However, the interaction site × gender is significant in case of spindle-shaped gall density (Table 1). Similarly, ANCOVA (with leaf length as the covariate) indicates that tree gender has no significant effect on the density of *S. betae* ($F_{1\text{-}93} = 3.43$, $P = 0.67$) and *S. wertheimae* ($F_{1\text{-}93} = 0.75$, $P = 0.78$).

DISCUSSION

Plant traits along the climatic gradient

Leaf size was remarkably small in the southern (xeric) relict populations in the Negev highlands (Fig. 2). This may suggest that the Negev populations suffer from adverse environmental conditions that have narrowed their distribution. Alternatively, smaller leaf size of the desert plants may reflect adaptation to dry environments (GIBSON 1998) and not stress. Indeed, the drier and hotter conditions in the Negev highlands had no effect on leaf developmental instability (Fig. 3).

Populations in the xeric habitats appear to have maintained their developmental stability. It is always possible that the traits measured were not sensitive to developmental instability

Table 2. Association between leaf traits and gall density presented as Pearson's correlation coefficient. All samples are of 96 trees, n.s. – non-significant, ** $P < 0.01$

	Missing leaflet	Leaf length	*S. betae*	*S. wertheimae*
Leaf asymmetry	-0.04 n.s.	-0.06 n.s.	0.15 n.s.	0.11 n.s.
Missing leaflet		-0.002 n.s.	-0.10 n.s.	-0.07 n.s.
Leaf length			0.26 **	-0.32 **
S. betae				-0.12 n.s.

detection. However, the results may actually suggest that the desert trees may be well adapted to their environment. Furthermore, in xeric habitats, *P. atlantica* mostly grow in wadis or high mountains such as in Sinai (Egypt), the Edom Mountains (Jordan) and the Negev Highlands, where the climate is cooler and the local macro- and microenvironments are less extreme (DANIN 1999, GICHUA et al. 2002). Even if the peripheral populations do suffer from stress, it may be the deviation from constant conditions and not the environmental conditions per se that increases instability (see LAPPALAINEN et al. 2000).

Insect density

Plant gender may interact with numerous biotic factors such as competitors, pathogens and herbivores (ÅGREN et al. 1999). In most cases, male plants suffer from higher levels of herbivory (BOECKLEN et al. 1990, BOECKLEN & HOFFMAN 1993). We detected no significant gender-related biases in the density of the galling aphids (see also HJÄLTÉN et al. 1993 for herbivory on *P. lentiscus*). Similarly, BOGEN et al. (1997) failed to detect gender-related differences in *S. wertheimae* density. They did show that *S. wertheimae* gall size was larger and contained twice as many aphids on male trees than on female. These differences may be the outcome of competition for resources between galls and fruits (WOOL & BOGEN 1999).

Developmental instability in *P. atlantic* had no noticeable relationship with gall density. Insect density was highly affected by the sites; *S. betae* is relatively rare in the Negev where *S. wertheimae* has established dense populations. The final galls of *S. betae* are formed on the leaflet margins, whereas galls of *S. wertheimae* are formed on the lateral buds (WERTHEIM & LINDER 1961). *S. betae* is therefore highly affected by vegetative reproduction, i.e. formation of new leaves in the spring (BURSTEIN & WOOL 1993, WOOL & BURSTEIN 1991). Therefore, modest production of vegetative growth in the Negev Highlands may limit the formation of *S. betae*'s galls. Indeed, we found a negative association between *S. betae* density and leaf size (Table 2).

Gender dimorphism

In *Pistacia* flowering occurs before vegetative development, and males tend to flower before females (protandry). Females invest more resources in reproduction (i.e., seed and fruits); males invest more resources in flowering early in the season before leaf production (DELPH 1999). So resources allocated to the development of vegetative growth, including photosynthetic tissues (leaf) in *P. atlantica* males, may be limited or unsteady. This may lead to greater developmental instability and increasing LA (EMLEN et al. 1993, MØLLER & SWADDLE 1997), and result in increased male LA as seen in this study (Fig. 5). Nevertheless because only five populations with relatively small samples were tested further research is clearly needed.

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