



# The effects of slope orientation on plant growth, developmental instability and susceptibility to herbivores

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## Abstract

South-facing slopes (SFS) may receive six times higher solar radiation than north-facing slopes (NFS). Although located only a few hundred meters apart, the microclimatic conditions on the slopes vary dramatically, affecting the biology of organisms at all levels. This study was conducted on both slopes of three canyons, where we examined leaf traits of *Pistacia lentiscus* L. and characterized the populations of its specific herbivore—the gall-forming aphid *Aploneura lentisci* Pass. Both a larger leaf size and lower gall density were found on NFS. However, gall size and leaf symmetry were not affected by slope. The unique biology of the aphids may explain their higher density on the SFS. Gall formers usually prefer and perform better on large plant organs (leaves), in accordance with the plant vigour hypothesis. Our results demonstrate that larger shaded leaves are an exception.

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## 1. Introduction

In the northern hemisphere, south-facing slopes (SFS) may receive as much as six times more solar radiation than north-facing slopes (NFS). Thus, the SFS has a more xeric environment, that is, warmer, drier and a more variable microclimate, than the mesic NSF. Although located only a few hundred meters apart and sharing

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the same macroclimatic zone, the microclimatic conditions on the slopes vary dramatically, affecting the biology of organisms at all levels (Nevo, 1997, 2001). The impact of slope orientation on the evolution, bio-diversity and ecology of numerous organisms has been extensively studied in the model system “Evolution Canyon” in Nahal Oren, Mt. Carmel, Israel.

The SFS is richer in paleotropical xeric biota, whereas the NFS has higher densities of mesic temperate species (Nevo, 1997, 2001). Plant cover and species community vary across slopes. In Nahal Oren, plant cover may reach 150% (as a result of overlapping life-forms, such as trees, shrubs, annuals, etc.) on the NFS, as compared with 35% coverage on the SFS. The slopes share less than 50% of vascular plant species (Nevo et al., 1999). The NFS has plant community dominated by trees and shrubs, whereas the SFS is predominantly composed of short-lived annuals (Nevo et al., 1999). Organisms that inhabit both slopes display genetic, morphologic, physiologic, and behavioural adaptive complexes in relation to each of the slopes (Nevo, 1997, 2001).

*Pistacia lentiscus* L. (Anacardiaceae) is an evergreen monoecious sclerophyllous shrub common throughout the Mediterranean (Zohary, 1952). The shrub is well adapted to xeric habitats (Liphshitz et al., 1985; Castro-Díez et al., 1998; Nevo et al., 2000) and can be found on both slopes, although it is dominant on the SFS (Nevo et al., 1999). This wide distribution across various climatic regions exposes local populations to differential growing conditions. Leaf morphology, physiology and chemistry of *P. lentiscus*, as well as the related species *P. terebinthus*, vary with climatic conditions (Castro-Díez et al., 1998).

Between slopes, sharp microclimatic differences may stress the plants and consequently their herbivores. A common method for measuring stress effects is to evaluate the organism's developmental instability (Møller and Swaddle, 1997). Indeed, Derzhavets et al. (1997) found increased instability (i.e. fluctuating asymmetry) on the Oren SFS in *Drosophila melanogaster*. Developmental stability is the ability of individual organisms to produce invariant phenotypes under different environmental conditions. Stability should be the greatest under optimal conditions and will decrease in sub-optimal conditions. Various biotic and abiotic factors, such as hybridization, elevation, pollution, competition, water and nutrient deficits, salt and shade, may increase plant developmental instability (Kozlov et al., 1996; Møller and Swaddle, 1997; Rettig et al., 1997; Roy and Stanton, 1999; Wilsey et al., 1998). The responses of herbivores to plant-growing conditions are variable and should be species-specific (e.g. Inbar et al., 2001). However, it is uncertain as to whether herbivores have a direct or an indirect relationship with host-plant developmental instability (Møller, 1995; Wiggins, 1997).

In this study, we addressed the following questions concerning possible microclimatic effects on *P. lentiscus* and the associated gall-forming aphid: (1) Do the microclimatic differences affect *P. lentiscus* leaf size? (2) Do the microclimatic differences affect the shrub's developmental instability (i.e. do they increase leaf asymmetry (LA))? (3) Do differential growing conditions on the two slopes have direct or indirect effects on the density and performance of a specialist gall-forming aphid?

## 2. Material and methods

### 2.1. The aphids

The gall-forming aphid, *Aploneura lentisci* (Pass) (Homoptera, Pemphigidae) forms kidney-shaped galls exclusively on *P. lentiscus* (Wool and Manheim, 1986, 1988). The galls are formed within 3 weeks, early in the spring, on the leaflet margin by the first instar nymphs hatching from over-wintering eggs. Within each gall, two additional generations of aphids are produced parthenogenetically. In the fall (September–November), a few hundred winged aphids (alate, fall migrants) complete their development and disperse from the galls. The subsequent generations develop on the roots of non-specific secondary hosts, mostly annuals and Gramineae. In the following spring, another winged morph (sexuparae) migrates back to the primary host *P. lentiscus* and produces sexual morphs. After mating, the fertilized eggs remain on the tree until the fundatrices hatch from them 1 year later (Wool and Manheim, 1986, 1988). The aphids are found throughout the geographical range of *P. lentiscus*. In Israel, galls can be found from the Galilee and Carmel mountains in the north to the Judean hills in the south (Inbar and Wool, 1995; Koach and Wool, 1977; Wool and Manheim, 1986, 1988).

### 2.2. Study sites

We examined *P. lentiscus* and the gall-forming *A. lentisci* populations at three sites (canyons): lower Nahal (meaning river) Oren and lower Nahal Mearot on Mt. Carmel, and Nahal Keziv in the upper Galilee (ca. 40 km north of Mt. Carmel). At each site, we randomly sampled 20 female shrubs on each slope (on the NFS of Keziv, however, only 10 shrubs were sampled). We focused on one plant gender to avoid gender-related biases in plant physiology, anatomy, developmental stability, and herbivory (Hjältén et al., 1993; Jonasson et al., 1997; Correia and Diaz Barradas, 2000). All samples were taken within ca. 1 km<sup>2</sup> on each slope during late August 2000.

### 2.3. Leaf sampling and measurements

From each shrub, we randomly collected 10 gall-free leaves from the middle of the current-year shoot. The leaves were taped onto a plant press and were allowed to dry before measurements. Leaf area was measured with a CI-202 digital leaf area meter (CID Inc., Vancouver, WA, USA). LA is a commonly used measure of plant developmental instability. LA reflects random and non-directional deviation from ideal bilateral symmetry (Emlen et al., 1993). Given that *P. lentiscus* has pinnate leaves, we measured LA (using a digital caliper) as the mean differences in the point of origin of the paired lateral leaflets (see also Freeman et al., 1993; Møller, 1998). The mean LA was divided by leaf length to standardize the values for size.

All measurements were taken by the same individual (MA). Thirty-five leaves were re-measured at least 1 week after the first measure. Repeatability ( $r$ ) was calculated

on the basis of a variance component derived from a one-way ANOVA (Lessells and Boag, 1987; Sokal and Rohlf, 1995). The analysis revealed high repeatability of the LA measurement ( $r = 0.99$ ,  $F_{34-69} = 480.5$ ,  $p \ll 0.01$ ). We used the proportion of presence/absence of the terminal leaflet as an additional indicator of stress-related developmental instability. *P. lentiscus* usually has paripinnate leaves that rarely obtain a small terminal leaflet (Zohary, 1952). The data are given as the mean percentage of leaves with terminal leaflets per tree.

#### 2.4. Gall-former density and performance

The number of galls was counted on 10 randomly selected shoots on each shrub. Gall weight of *A. lentisci* correlates significantly with aphid reproductive success (Wool and Manheim, 1988) and therefore was considered as a reasonable index for the aphid's performance and fitness. If present, 10 randomly selected galls were collected from each shrub. Galls were oven-dried at 70°C for a week before weighing.

#### 2.5. Data analyses

The data were analysed using a two-way ANOVA, with site and slope as main effects. Data on LA and percentage of leaves with a terminal leaflet were log- and arcsine transformed, respectively, prior to analysis. Associations between leaf traits and gall density and weight were examined using Pearson's correlations (Sokal and Rohlf, 1995). All statistical analyses were performed with 'Statistica' software for Windows (StatSoft Inc., Tulsa, OK, USA).

### 3. Results

#### 3.1. Plant traits

Leaf size was greatly affected both by site and slope (Fig. 1, Table 1). Leaf size at the Oren site was larger than at Keziv (37%) and Mearot (24%). Within sites, slope had a dramatic effect on leaf size, which was significantly smaller (by 20% on average) on the SFS. Across slopes, differences were not restricted to leaf size, as it appears that the shrubs on the NFS were taller (unpublished observations).

On average, 18.9% (range: 11.9–23%) of the leaves had terminal leaflets. However, terminal leaflet presence was not affected by slope, site, or the interaction among them (Table 1). Overall, LA was not affected by site or slope (Fig. 2, Table 1). However, the trend is more complex: LA was similar on both slopes of Mearot and Keziv, whereas LA at the Oren site was two times higher on the SFS than on the NFS ( $t = 2.04$ ,  $df = 38$ ,  $p = 0.05$ ; Fig. 2). The large differences in values at the Oren site may indicate that an additional local factor on the SFS caused developmental instability (LA), as reflected by the nearly significant slope  $\times$  site effects in the ANOVA analysis (Table 1). Leaf size was positively correlated with LA, even when size was standardized (Table 2).

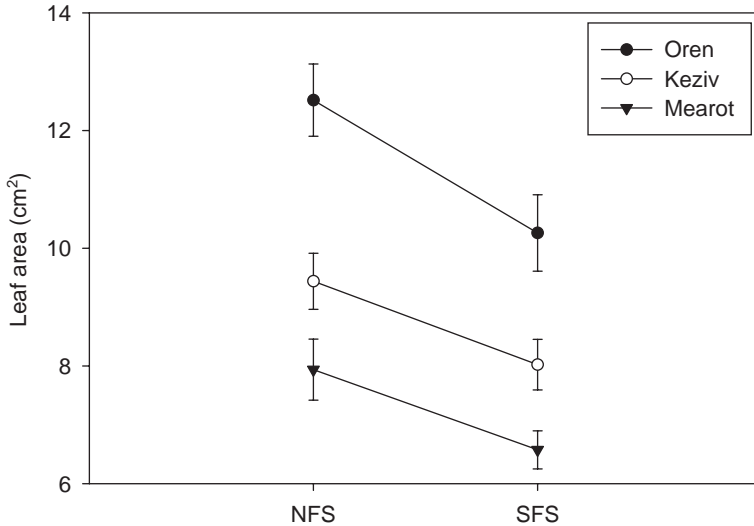


Fig. 1. Mean ( $\pm$ S.E.) *Pistacia lentiscus* leaf area across sites (legends) for the south-facing slopes and north-facing slopes. See Table 1 for statistical analysis.

### 3.2. Gall-former density and performance

Gall density was affected by site, with the densest populations being observed at Mearot (Fig. 3). In contrast to our findings on leaf size (Fig. 1), the populations of the gall-forming aphids were consistently higher on the SFS (Fig. 3, Table 1), resulting in a negative correlation between leaf size and gall density (Table 2). Gall density on the Keziv SFS was nearly 16 times higher than the density on the NFS, which was close to zero. Similarly, gall density on the SFS was higher in Oren (4.3) and Mearot (2.4) than on the NFS. Gall weight (i.e. insect performance), on the other hand, was not significantly affected by slope or site (Fig. 4, Table 1), although gall weight had an overall positive association with gall density (Table 2).

## 4. Discussion

The microclimatic differences between the NFS and the SFS had no effect on leaf developmental instability, as measured by LA and the presence/absence of terminal leaflets. On each slope, *P. lentiscus* faces different environmental challenges. On the NFS, it is understory shaded by the dominant trees, such as *P. palaestina* and *Quercus calliprinos* (Nevo et al., 1999). Light-limited NFS shrubs develop “shade leaves” that are larger (Fig. 1), with a thicker palisade layer that increases light trapping (Nevo et al., 2000). On the other hand, *P. lentiscus* is dominant in and adapted to xeric Mediterranean conditions (Castro-Díez et al., 1998). Shrubs on the SFS are adapted to a dryer and warmer microclimate; their leaves are xeromorphic, with smaller size and thicker epidermis (Nevo et al., 2000).

Table 1

Two-way ANOVA table summarising the effect of site and slope on *Pistacia lentisci* leaf traits, the density and performance of the gall-forming aphid *Aploneura lentisci*. Because some shrubs did not bear any galls, the df error of gall weight analysis is smaller

	df effect	df error	<i>F</i>	<i>p</i>
<i>Leaf asymmetry</i>				
Site	2	104	1.47	0.23
Slope	1	104	3.30	0.07
Site × Slope	2	104	2.83	0.06
<i>Terminal leaflet</i>				
Site	2	104	0.41	0.66
Slope	1	104	0.01	0.93
Site × Slope	2	104	0.15	0.86
<i>Leaf size</i>				
Site	2	104	33.76	≤0.01
Slope	1	104	14.05	≤0.01
Site × Slope	2	104	0.46	0.63
<i>Gall density</i>				
Site	2	104	7.83	≤0.01
Slope	1	104	41.77	≤0.01
Site × Slope	2	104	0.08	0.92
<i>Gall weight</i>				
Site	2	75	1.93	0.15
Slope	1	75	0.11	0.73
Site × Slope	2	75	0.11	0.89

Interpretation of stress and the resulting LA in long-lived shrubs naturally exposed to low resources is problematic. These plants may be well adapted, both physiologically and genetically, to the local harsh conditions (e.g. Escós et al., 2000). However, the deviation from “normal conditions,” rather than the harsh environmental conditions per se, may increase instability. The importance of deviation from normal conditions in increased developmental instability was recently demonstrated in white birch (*Betula pubescens*) leaves, with an increase in LA following increase in plant resources (i.e. experimental fertilization) (Lappalainen et al., 2000). Nevertheless, the influence of these various factors on the developmental instability of *P. lentiscus* should be tested in a common garden-controlled experiment (see Wilsey et al., 1998).

Developmental instability (i.e. LA and the presence/absence of a terminal leaflet) had no significant relationship with either gall density or gall weight (Table 2), indicating that the gall induction process of development is not affected by nor does it cause leaf asymmetry. The relationships between LA and herbivory vary among systems (Møller, 1995; Wiggins, 1997). In trying to resolve the controversy, Lempa et al. (2000) argued that the relationships between developmental instability and

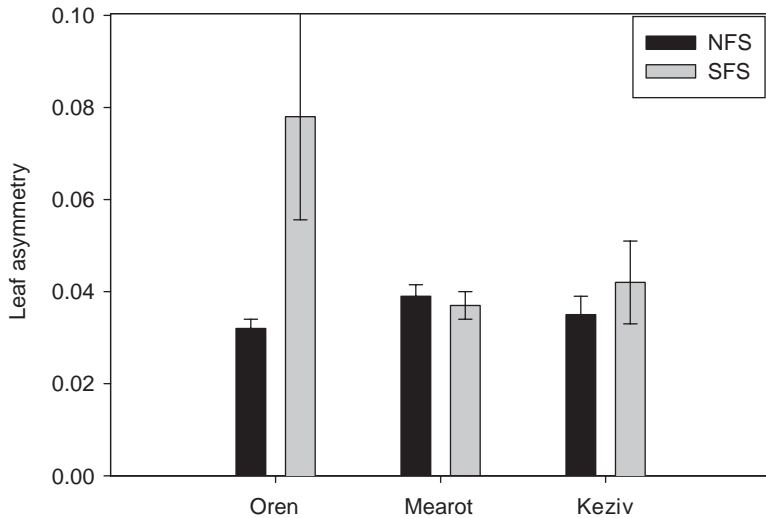


Fig. 2. Mean ( $\pm$ S.E.) leaf asymmetry (LA—mean deviation from the origin of parallel leaflets), as an indicator of developmental instability. Note the large increase of LA on the south-facing slope (SFS) of the Oren site.

Table 2

Association between leaf traits and gall density presented as Pearson's correlation value— $r$  (sample size in brackets)

	Leaf asymmetry	Gall density	Gall weight
Leaf size	0.18 (110)*	−0.25 (110)**	0.03 (81) ns
Leaf asymmetry		0.09 (110) ns	0.02 (81) ns
Gall density			0.23 (81)*

ns—non-significant.

\* $p < 0.05$ .

\*\* $p < 0.01$ .

herbivory may depend on the linkage between LA and certain biochemical pathways. If LA is associated with defensive compounds, then the outcome will be reduced herbivory. However, it is also possible that LA may be associated with biochemical pathways that increase herbivore performance.

Presence of a terminal leaflet and leaf LA were not affected by site or slope (Table 1). One exception was the LA on the SFS at the Oren site (Fig. 2), which was nearly twice the size of that on the NFS. These results indicate that the *P. lentiscus* shrubs on Oren's SFS were exposed to additional environmental pressure(s). Indeed, this location is subject to occasional cattle grazing (personal observations) that may increase LA (Martel et al., 1999; Escós et al., 2000; Olofsson and Strengbom, 2000). It is also possible that there are significant differences in the biotic conditions, such

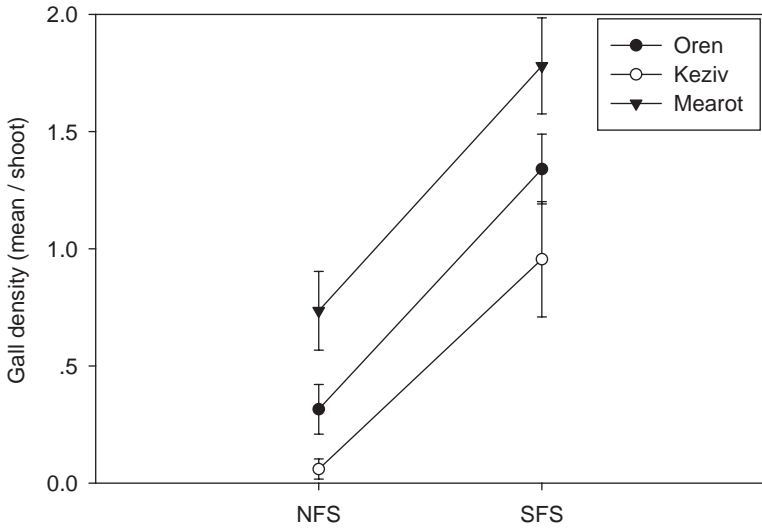


Fig. 3. Mean ( $\pm$ S.E.) galls/shoot/tree of *Aploneura lentisci* on *Pistacia lentiscus* across sites (legends) and slope orientation (X-axis).

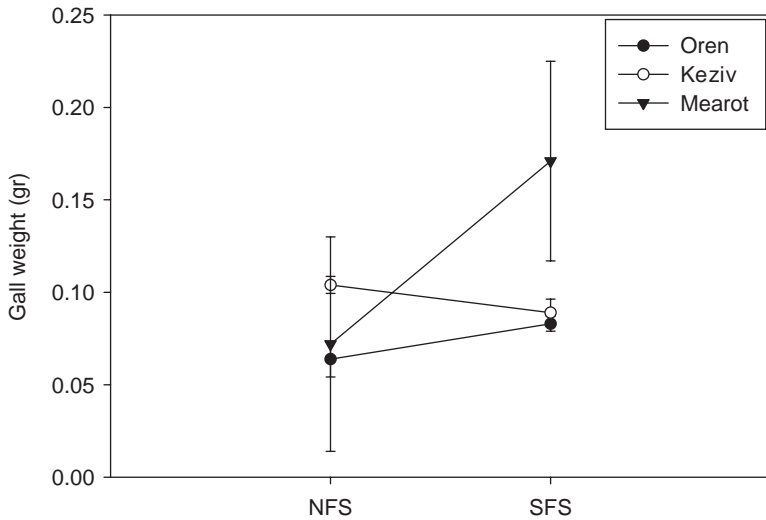


Fig. 4. Gall dry weight (mean  $\pm$  S.E.) across sites and slopes as an indicator of aphid reproductive success. Note that due to high variance between sites (legends) and slope orientation within sites (X-axis), comparisons are not statistically significant (see also Table 1).

as solar radiation on the slopes of the three canyons. Nevertheless, it should be emphasized that the increased LA at this location did not affect the aphids' density and performance.

What causes higher gall densities on the SFS? The fact that aphid reproductive success was not affected by slope-related conditions suggests that differences in between-slope gall density were not associated with active selection of a superior host by the aphids. Several factors may cause the pronounced differences in gall density between slopes. The first set of factors may involve the crucial stage in the *A. lentisci* life cycle, with the re-migration of the sexuparae that developed at the roots of the secondary hosts to its primary host (*P. lentiscus*). The non-specific secondary hosts of *A. lentisci* and other Fordinae species are various annual and perennial grasses (Gramineae) (Wool and Manheim, 1986, 1988; Wool et al., 1997). In comparison with the NFS, the warmer and xeric SFS has higher plant diversity (Nevo et al., 1999) and is predominated by winter- and spring-growing annuals (Nevo et al., 1999), which are potential secondary hosts for *A. lentiscus*. Thus, the SFS may carry a larger pool of aphids on the secondary hosts.

Once emerging from the roots of its secondary hosts, the sexuparae face the task of finding the *P. lentiscus* shrubs (Wool et al., 1997). This task is not trivial, and many aphids fail to locate the correct host. Among several species examined, the sexuparae of *A. lentisci* had the least capability of finding a host, frequently choosing the wrong host (Wool et al., 1994). *P. lentiscus* is a major shrub on the SFS, where it forms a typical community with *Ceratonia siliqua* (Caesalpiniaceae) (Nevo et al., 1999). Thus, it is possible that it can be found relatively easily by the sexuparae. In addition, the much less frequent *P. lentiscus* shrubs on the NFS are covered with canopies of the dense community of *P. palaestina* and *Quercus calliprinos* (Nevo et al., 1999). Masking by higher and denser plants makes it much more difficult for the sexuparae to find the host. Neighbouring plants therefore may act as “defence guilds by providing repellents or masking feeding and host selection cues (Reviewed by Atsatt and O’Dowd, 1976).

The second set of factors may be plant-related. The climatic differences could affect the chemical and physical susceptibility/resistance of the hosts. We plan in the future to examine the nutritional and chemical defence contents, as well as water potential, of *P. lentiscus* on both slopes. As gall can be formed only on young undifferentiated leaves, synchronization between the aphids and plant phenology is crucial (e.g. Burstein and Wool, 1993). Some plants on the warmer SFS develop earlier than do those on the NFS (G. Neeman, pers. comm.). It will be worth testing whether microclimatic slope-related differences could break the aphids’ synchronization with the plant growth phenology.

In line with the plant vigour hypothesis, gall-forming insects usually prefer large and fast-growing plant organs, such as leaves and shoots (Price, 1991; see also Koricheva et al., 1998). Leaf size can predict gall success (Whitham, 1978). Indeed, the galls of *A. lentisci* tended to be heavier in shoots with many leaves (Wool and Manheim, 1988), but we found that leaf size did not predict gall density or success. In the current study system, leaf size does not necessarily represent growth vigour, but rather adaptation to light limitation by formation of larger ‘shade leaves’ (e.g. Moore et al., 1995) on the NFS. Accordingly, it is necessary to measure leaf growth rather than leaf size per se (usually measured at the end of the season), since the latter may be misinterpreted as a sign of vigour.

## 5. Summary

South-facing slopes (SFS) may receive six times the amount of solar radiation than that received by north-facing slopes (NFS). Consequently, they are more xeric (warmer and drier). We examined slope effects on the leaf traits of a plant that may be associated with the density and reproductive success of a host-specific gall former. Leaf samples of *Pistacia lentiscus* L., a dominant evergreen shrub in the Mediterranean maqui, were taken in the north- and south-facing slopes of three canyons. Similarly, we examined the density and gall size of the gall-forming aphid *A. lentisci* Pass. A two-way ANOVA revealed larger leaf size, but lower gall density on the NFS. Gall size was affected by site (canyon), but not by slope. Leaf developmental instability, a common indicator of plant stress, was examined by measuring leaf asymmetry (LA), the deviation of origin of the paired lateral leaflets, and the absence of terminal leaflets. Leaf asymmetry was not affected by slope and was not associated with gall density or size. It is suggested that the higher abundance of the aphids' secondary hosts (mainly Gramineae) and the dominance of the aphids' primary host, *P. lentiscus*, on the SFS are responsible for the higher gall density there. In addition, shading and masking by neighbouring plants in the dense forest on the NFS may make the shrubs difficult to find for small migrating aphids. Usually, gall formers prefer larger plant modules. When leaves are larger due to shade effect, however, 'shade leaves' (as on the NFS) may not be a favourable substrate for gall induction and development.

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