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Complex architecture of *Tamarix nilotica* and resource utilization by the spindle-gall moth *Amblypalpis olivierella* (Lepidoptera: Gelechiidae)

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ABSTRACT

Tamarix nilotica and the spindle-gall moth, *Amblypalpis olivierella* Rag., were studied to test the hypothesis that gall-inducing larvae utilize the most vigorous plant modules available on individual host plants. Five trees were studied in the vicinity of Caesarea, Israel, and the complexity of their architec- ture and phenology described. Four types of shoot were recognized: pendu- lous, upright, short, and bole sprouts. Three phenological conditions of shoot growth were categorized: (1)active meristematic growth; (2)dormant shoots; and (3) short shoots, which were particularly young and actively growing. The general response of gall initiation in relation to shoot-length classes per tree was unique for each tree, depending upon the frequency of the different shoot types available as resources. Only vigorously growing shoots were utilized by larvae, which invaded shoots just behind active meristems. Young *Tamarix* with mainly upright and active shoots supported an exponentially rising attack rate with increasing shoot-length class. Large mature trees with more heterogeneous architecture and shoot types illustrated gall patterns in relation to shoot- length categories that were significant or not significant depending on shoot type, but attack was invariably concentrated on meristematically active shoots in the tree canopies. Where very vigorous basal sprouts were present, in pruned trees in landscaping, these were attacked at a low frequency. Thus, the plant vigor hypothesis is supported if examined in relation to the meristematic activity of shoots at the time of attack, but simpler patterns in relation to shoot-length classes, observed so frequently in north temperate systems, are obscured by the architectural complexity of these Mediterranean climate trees.

INTRODUCTION

For small herbivores the host plant provides both food and habitat. Therefore, the way the plant grows is of central concern in understanding the plant-herbivore interaction. Plants, being modular organisms composed of populations of similar parts such as

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Author to whom correspondence should be addressed. E-mail peter.price@nau.edu leaves, buds, and stems (Harper, 1977, 1981), develop a highly predictable architecture onto which the feeding pattern of the herbivore becomes superimposed. Not only is the architecture predictable, but the timing or phenology of the display of parts usually shows clear patterns in the production of young shoots and leaves, and mature modules (e.g., Niemelä and Haukioja, 1982). Therefore, understanding plant growth and structure is fundamental to understanding how a herbivore is adapted to exploiting plant resources (Haukioja et al., 1990; Haukioja, 1991). Frequently these resources may be ordered as independent variables on gradients of module size (e.g., Price et al., 1995), module phenology (e.g., Niemelä and Haukioja, 1982), or chemical concentrations in modules (Zucker, 1982) in order to evaluate the response of herbivores. Therefore, ecological concepts, hypotheses, and theories that address plant and herbivore interaction should encompass plant modular growth as a basic variable to which herbivores must respond in evolutionary and ecological time (Haukioja, 1991; Price, 1991; Price et al., 1997).

The large majority of studies on herbivores in relation to plant architecture are relevant to north temperate regions (e.g., Lawton, 1983; Senn et al., 1992; Price et al., 1997), in which the phenology of module development is highly predictable and largely synchronous for each plant species (e.g., Niemelä and Haukioja, 1982; Slansky and Scriber, 1985). However, as warm growing seasons become longer at lower latitudes, in many plant species phenological development become more complex and unsynchronized, making the analysis of herbivore responses to plant modular structure more challenging. Modules on a single plant may be in very different stages of development, from dormancy, to new growth, to well-developed modules. For example, in Israel many areas, such as the coastal plain from Tel Aviv to Haifa, have climates with 4–5 months of rainfall and 8–10 months with temperatures averaging above 10 °C, providing enough time per year for a wide variety of patterns in module development and phenology to evolve. Phenological variation among trees in the same population has been found to be very high in some species in Mediterranean climates (e.g., Orshan, 1989; Ne'eman, 1993). However, phenological heterogeneity within individual trees is not well studied and we base our statements on personal observations while sampling gall-inducing insects around the world (cf. Price et al., 1998, for locations).

Gall-inducing insects are particularly sensitive to modular development of the host plant because the program for differentiation of tissues during growth is diverted early in module development to the creation of a gall. Thus, the more diversified the phenology of module production and size becomes, as in warm temperate to tropical climates, the more likely it is that life histories of gall-inducing insects will evolve to respond to the less predictable or less synchronized display of resources that the host plant population provides. This increased complexity of module production and herbivore response has not been investigated before, as far as we know, so we exploited the opportunity to study the modular development and architecture of *Tamarix nilotica*, the resources it provided for the spindle-gall moth *Amblypalpis olivierella* Rag. (Lepidoptera: Gelechiidae), and the response of the herbivore to the host plant.

We asked the following questions in our study: (1) what is the architecture of *T. nilotica* and how does it develop in terms of shoot and stem modules, i.e., the pattern and phenology of growth? (2) What are the essential resources provided by the plant for the spindle-gall moth, and how are these resources utilized?

We consider these questions to be important because the answers will contribute to our long-term research goals of understanding the relationship between insect herbivore life history traits, their consequent utilization of plant resources, and ultimately their population dynamics (e.g., Price et al., 1998). In particular, we wished to test the Plant Vigor Hypothesis (Price, 1991), which argues that many insect herbivores select and utilize the most vigorous plants or plant modules available, on which larvae perform best in terms of growth rate and/or survival. This contrasts with the older hypothesis developed by White (e.g., 1969, 1984) suggesting that insects perform best on stressed plants, although no doubt there is a continuum of responses along the gradient from vigorous to stressed plants (Larsson, 1989; Koricheva et al., 1998; see also White, 1993). *Amblypalpis* provided an interesting case because females do not make choices on where galls are initiated, they show no preference for long shoots (Lupo and Gerling, 1984; see also next section), and the distribution of galls appeared to be independent of shoot length, shoot length being an indication of module vigor. Hence, this species appeared to be an exception to a pattern we have found frequently (e.g., Craig et al., 1989; Price et al., 1990, 1998; Price, 1994). The many species showing patterns consistent with the plant vigor hypothesis help to answer the old question on why the world is green (Hairston et al., 1960): because only the longest, most vigorous, and rarest plant modules are actually utilizable by many herbivores, for various reasons. An ancillary reason for studying this species is its potential for use in the biological control of *Tamarix* in the United States (cf. DeLoach et al., 1996).

STUDY ORGANISMS AND STUDY SITES

Tamarix nilotica is a common tree in Israel frequently used in the stabilization of sand dunes along the coast, and as a tree in landscaped areas. It grows well in sandy and salty soils, reaching a height of 25 m or more. We concentrated studies on trees growing in the vicinity of Caesarea (Qesarya)—on the coast between Tel Aviv and Haifa. The trees were growing on Kibbutz Sedot Yam and on land adjacent to the remains of the Roman city of Caesarea (32°30′N, 34°54′E). Five trees were studied: two mature, large trees that had grown in a natural manner, with very little pruning; two trees with low, rapidly-growing ramets and unpruned; and one large tree in a parking lot that had been pruned persistently for many years, producing a large bole, from which young shoots grew, and a large crown with normal architecture.

The life history of the spindle-gall moth has been described by Lupo (1979) and Lupo and Gerling (1984), and is summarized in Fig. 1. Illustrations of young and fully developed galls are provided in Lupo and Gerling (1984). Briefly, adults emerge in November and December, eggs are placed in crevices in the bark during December, and larvae begin to hatch in March, boring into developing shoots and initiating gall formation, with galls becoming clearly visible in May. Galls grow and larvae develop from March to August, and pupation in the gall occurs in September.

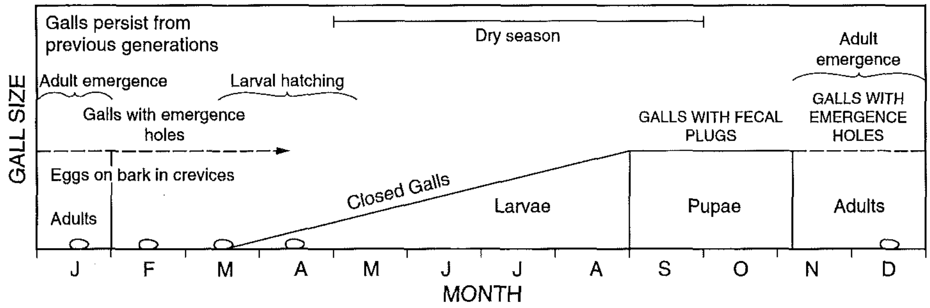

Fig. 1. Life cycle of *Amblypalpis olivierella*, based on Lupo and Gerling (1984), with modifications added from the present study.

Therefore, larvae select gall sites, not females, and females oviposit long before shoot quality for gall formation can be evaluated.

Our studies were conducted during May 1998, and synchronized with the end of gall initiation so that the condition of shoots being attacked by the majority of the population could be assessed. The large majority of larvae at this time were in the first instar, with a small proportion in the second instar.

The Mediterranean climate at the coastal study site is characterized by warm, wet winters, with temperatures about 10–25 °C and rainfall ranging from 50 to 175 mm per month, and by hot, dry summers with temperatures in the range of 25–35 °C and with minimal precipitation. In the month of May, during the study, the season was advancing rapidly into the dry, hot period of summer.

METHODS

To address question 1 on the architecture of *Tamarix*, we employed three scales: the whole form of the tree, the branch characteristics, and the individual developing shoots available to the larvae of the moth. The gross form of each tree was photographed, and projected images were traced onto paper. These silhouettes of branching patterns provide a general view of how the sample trees differ in architecture, how the tree develops, and the kinds of shoots available as resources for moth larvae. The five trees used were selected as representative of the main types in the vicinity of Caesarea: mature trees, younger and lower growth in an open habitat, and a tree with a pruned bole having a mature canopy above and young shoots arising from the bole. We use standard terminology in this paper for the branching system of woody plants. A *shoot* is the stem plus leaves growing in the current season, or the most recent growing season. A *stem* is an axis of growth that may be developing in the current growing season or may be older, showing up to several years of growth, after which we use the word *branch* to designate major architectural features with several to many years of growth.

At the smaller scale, at least five branches, about 5–6 years old, were taken haphazardly from about 2–3 m from the ground. Ages of stems were estimated by counting back from new shoots the number of major branch nodes, which indicated the number of times a new growing season had occurred. Some of stems we cut, dried, and sanded with fine sandpaper to reveal the growth rings that are distinct only with this kind of preparation. Estimates of stem age using growth pattern and growth rings for stems 1–6 years old were identical or within 1 year of each other. The manner in which shoots were positioned was recorded as pendulous, upright with apical growth, or with growth from dormant buds as on older stems. These categories will become clear in the Results section.

At the smallest scale, shoots that had developed or were developing within the growing season were then sampled haphazardly, and length was measured to the nearest centimeter. This sample then provided an estimate of the shoot-length distribution developed by each tree. A record was kept of shoots that were actively growing with lighter green foliage and those that had ceased to grow with darker foliage at the shoot tips. At least 250 shoots were sampled from each tree, with a maximum of 343 shoots sampled on one tree.

With these methods the rather complex and variable architecture of each tree was categorized in terms of the way in which resources developed for utilization by the gall-inducing larvae.

To answer question 2 on the resources utilized by larvae, a record was kept of all galls formed on shoots in the shoot sample described above: the shoot length, location of each gall, number of galls per shoot, and the shoot type and condition of growth. At least 100 galls were recorded for each tree, with a maximum of 512 galls on one tree. For each tree individually we searched for patterns of attack by the gall former in relation to the gradient of shoot-length classes, with classes covering 5 cm. Shoot-length class was used as the independent variable (x) and mean number of galls per shoot (y) as the dependent variable, and the regression model providing the highest r^2 value, or estimate of the amount of variance accounted for, was used in figures. The number of shoots sampled in each shoot-length class was also plotted, enabling an evaluation of the display of shoots on a tree and the pattern of attack on those shoots. Shoot-length class data were combined when fewer than five shoots per class were sampled.

RESULTS

Tamarix architecture

At the time of gall initiation in March to May, any tree provides a very heterogeneous array of shoots on which larvae must forage. Not only is there a wide range of shoot lengths indicating different levels of vigor in the canopy, but on older trees there are pendulous shoots and more upright shoots, and shoots that have stopped apical growth and those that remain in an active state. For this paper we designate shoot types as *P* for pendulous, *U* for upright, *a* for actively growing, and *d* for dormant. The general architecture of a large tree allowed to grow more or less normally without pruning is therefore composed of upright trunks and lower branches with an increasing tendency for distal branches to become more pendulous (Fig. 2). Thus, many shoots available for attack by larvae are also pendulous.

Fig. 2. General architecture of a large *Tamarix* tree grown in the absence of much pruning (*left*); a young *Tamarix* tree (*middle*), showing a majority of *Ua*-type shoots; and a large *Tamarix* tree growing in a parking lot and pruned to one main heavy trunk (*right*). Note the many basal shoots (*Ba* type) on the bole of the tree. Trees are not drawn to the same scale. Dashed lines and arrows indicate the location of sampling in the canopies.

At the edge of the canopy with pendulous branches, in full sunlight some new shoots become more upright and grow more robustly than pendulous shoots. New shoots may be initiated also on older stems, such that at the time of gall formation many short, young, and vigorously growing shoots are available on the upper aspect of a branch. These shoots are designated as *Sa* for short and active.

Younger *Tamarix* trees or ramets growing in full sunlight develop with an upright ascendant branching pattern with the large majority of apical meristems directed toward the light (Fig. 2). Pendulous stems and shoots are rare, and shoots initiated from long-dormant buds on older stems are generally absent.

When *Tamarix* is grown as a landscape tree in parks, gardens, and parking lots, trees are usually pruned to form a single bole that grows to a large diameter (Fig. 2). From the bole many new shoots are sprouted in profusion and these grow exceedingly vigorously, some reaching over 1 m in length in a growing season. While the tree canopy remains as described for large trees, the sprouting shoots provide yet another dimension to the shoot heterogeneity to which gall-initiating larvae are exposed. Such shoots are designated as *B* for bole and all were actively growing (*a*).

Any one shoot in one growing season offers a rapidly expanding number of meristems producing resources suitable for larval utilization. A very young and therefore

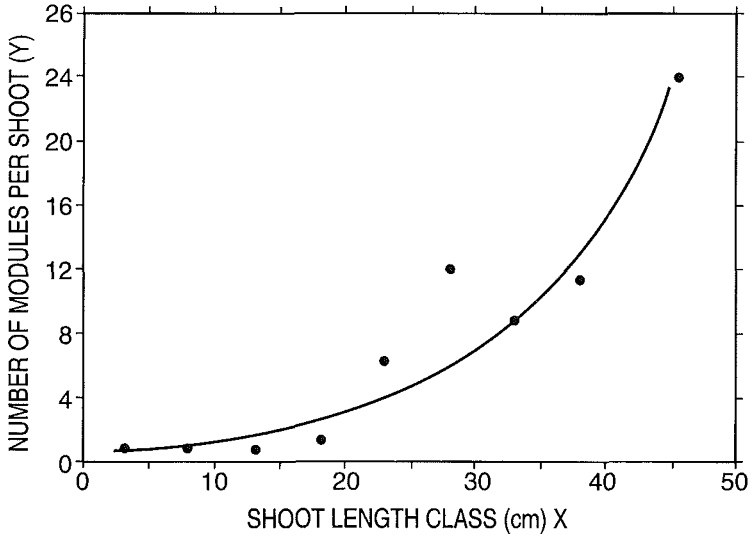

Fig. 3. Mean number of modules per shoot in relation to shoot-length classes indicating the exponentially increasing number of gall sites available as active shoots develop. Based on 67 *Ua*-type shoots in 9 shoot-length classes.

short shoot has basically one location for a gall, on the main axis. As the shoot elongates, more lateral meristems become active, producing lateral axes available for gall formation. And these lateral axes may produce more axes of growth, forming a pattern of meristems and shoots reminiscent of a complex fern frond. In this way the number of locations on a developing shoot available for gall formation increases exponentially as the shoot elongates (Fig. 3; $y = 0.58e^{0.08x}$, $r^2 = 0.89$, $n = 9$, $p < 0.01$).

The heterogeneity of shoots available when larval spindle-gall moths are foraging is important to appreciate when searching for patterns of attack. Therefore, while we used a general shoot-length class axis for plotting responses of larvae to shoot length, we also kept track of the different kinds of shoots that were sampled and larval response to these shoot types.

Resource utilization by gall-inducing larvae

Galls were initiated very close to apical meristems of shoots, often within 1 cm of the shoot tip. Considerable distortion of shoots resulted from uneven development of galls on young and rapidly developing shoots. Larvae initiated galls on the youngest possible growth behind the strongest meristems. These general observations were supported by the quantitative analyses using shoot-length class as the independent variable, although the broad patterns varied according to the type of tree studied and the predominant kinds of shoots available. Therefore, each tree is treated individually in these results, starting with the two large trees.

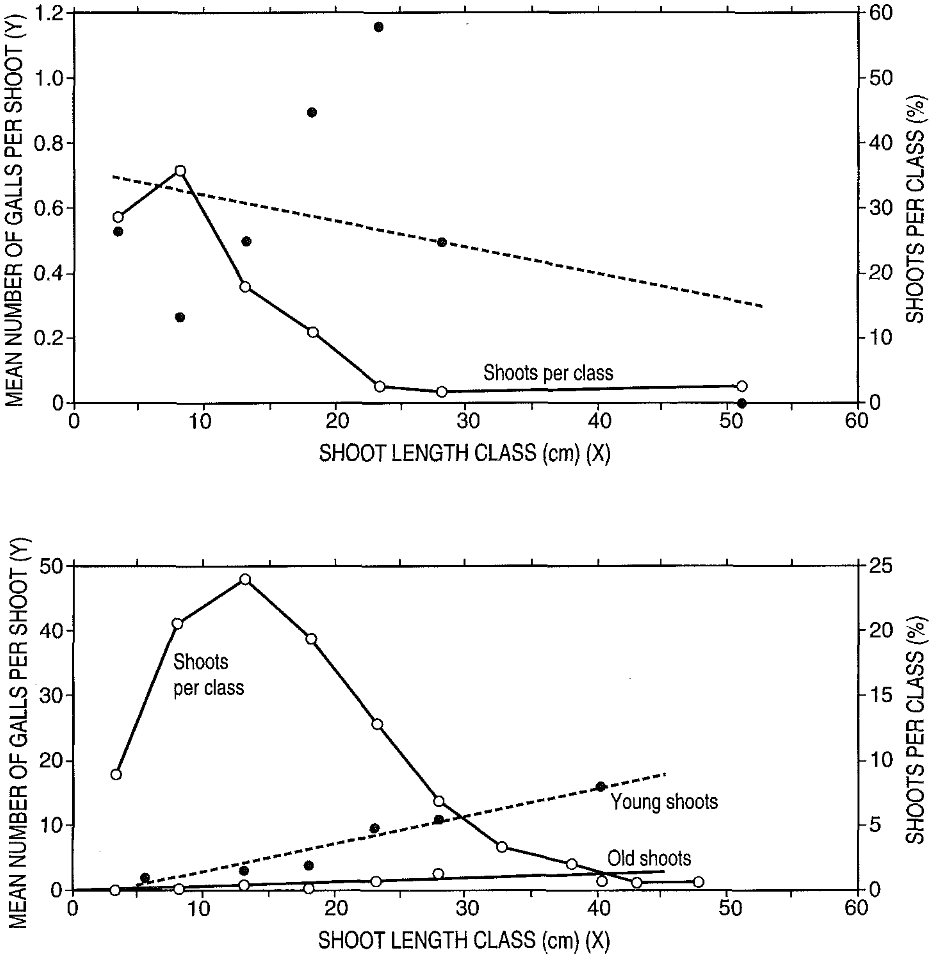

Fig. 4. Distribution of shoots and mean number of galls per shoot (y) in relation to shoot-length class (x) in Tree 1 (above) and Tree 2 (below), both large, mostly unpruned trees. In Tree 1, *Sa* shoots predominated in the 0–10 cm class, *Ua* shoots in the 10–30 cm classes, and *Pd* shoots in the 30+ cm classes. In Tree 2, a few *Ua* shoots were available, but the pattern in young shoots was developed mostly in *Pa* shoots. Old shoots were all *Pd* type. Based on 381 shoots and 183 galls in 7 shoot-length classes for Tree 1; 302 shoots, 512 galls and 6 and 7 shoot-length classes for active and dormant shoots, respectively, for Tree 2.

In Tree 1, an old unpruned tree with decumbent branches and shoots in the canopy near the ground, there were also many upright rapidly growing shoots developing from the top of decumbent branches (types *Ua* and *Sa*). The distribution of shoots was heavily skewed to short shoots in the 1–15 cm classes, with rapidly decreasing frequency of longer shoots over 20 cm (Fig. 4). Frequency of gall formation was displaced well to the right of a pattern expected from random attack, the observed frequencies being significantly different from those expected if random attack had occurred ($\chi^2 = 99.01$, $n = 7$, $p < 0.0005$). However, regression analysis showed no significant trend of attack in relation to shoot length ($y = 0.72–0.01x$, $r^2 = 0.11$, $n = 7$, N.S.), with a slightly negative trend. The pattern of attack was generated by the many type *Sa* shoots, and *Ua* shoots in the ranges of 1–10 cm and 10–30 cm, respectively, with *Pd* shoots predominating in longer shoot-length classes. The pattern shows that later in the dry season when shoot development has stopped, a false impression may be reached that larvae were relatively unspecific in the length of shoot attacked, an impression certainly obtained by casual observation of mature spindle-gall distributions on trees. However, this analysis shows that when the varieties of shoot types and phenologies are recognized, larvae initiate galls only on the most actively growing shoots, whatever their actual length may be.

On Tree 2, another old and unpruned tree within 10 m of Tree 1, the patterns of shoot availability and attack were very different from Tree 1 (Fig. 4). Type *Sa* shoots were almost absent, *P*-type shoots were most common, and *Pa* and *Pd* shoots were present, but some *Ua* shoots were also available for attack. When the *a*-type and *d*-type shoots were segregated in the analysis there was a clear and significant trend of increasing number of galls per shoot as shoot-length class increased in the *a*-type shoots, with more galls on active than dormant shoots (*a*-type: $y = 0.42x–1.39$, $r^2 = 0.93$, $n = 6$, $p < 0.01$; *d*-type: $y = 0.04x–0.09$, $r^2 = 0.52$, $n = 7$, N.S.). We assume that galls on *d*-type shoots had been initiated while the shoot was still actively growing. This kind of pattern of attack, increasing with shoot length, is more characteristic of patterns seen in north temperate systems, as discussed in the Introduction.

Trees 3 and 4 were younger trees with upright architecture and ascendant apical meristems. Tree 3 had branches about 5 years old with shoots at 2.5 m above ground level, with most shoots of the *Ua* type. Tree 4 was about 3 m tall with a mixture of *Ua* and *Ud* shoots, which were distinguished in the analysis. In both cases, active shoots were increasingly attacked as shoot length increased (Fig. 5), as predicted by the pattern of shoot development described in Fig. 3 (Tree 3: $y = 0.01e^{0.15x}$, $r^2 = 0.96$, $n = 7$, $p < 0.01$; Tree 4, *Ua* shoots: $y = 0.23e^{-0.08x}$, $r^2 = 0.91$, $n = 6$, $p < 0.01$). These younger trees with simpler architecture illustrated more consistent patterns than Trees 1 and 2.

Tree 5 provided the added complexity of *Ba*-type shoots, with rapidly growing, sprouting shoots from the bole of the tree. However, *Sa* shoots were very rare and hardly influenced the general pattern of attack, contrary to conditions in Tree 1. Many *P*-type shoots were actively growing. While shorter shoot-length categories were more strongly represented in the canopy, as in the general case, attacks and gall formation increased exponentially with shoot-length class (Fig. 6; $y = 0.05e^{0.10x}$, $r^2 = 0.72$, $n = 10$, $p < 0.01$). *Ba*-type shoots occurred in the shoot-length classes from 30 to 120 cm, most commonly in the range of 40–65 cm. Levels of attack were generally low in *Ba*-type shoots, and when all shoots on Tree 5 are considered, there is no significant trend in attack relative to shoot-length class ($y = 0.74 + 4.40e^{-3x}$, $r^2 = 0.02$, $n = 14$, N.S.). Again the specific characteristics of shoot types on a single tree are critical in the detection of pattern. More detail on the nature of larval utilization on *Ba*-type shoots is provided in the caption of Fig. 6.

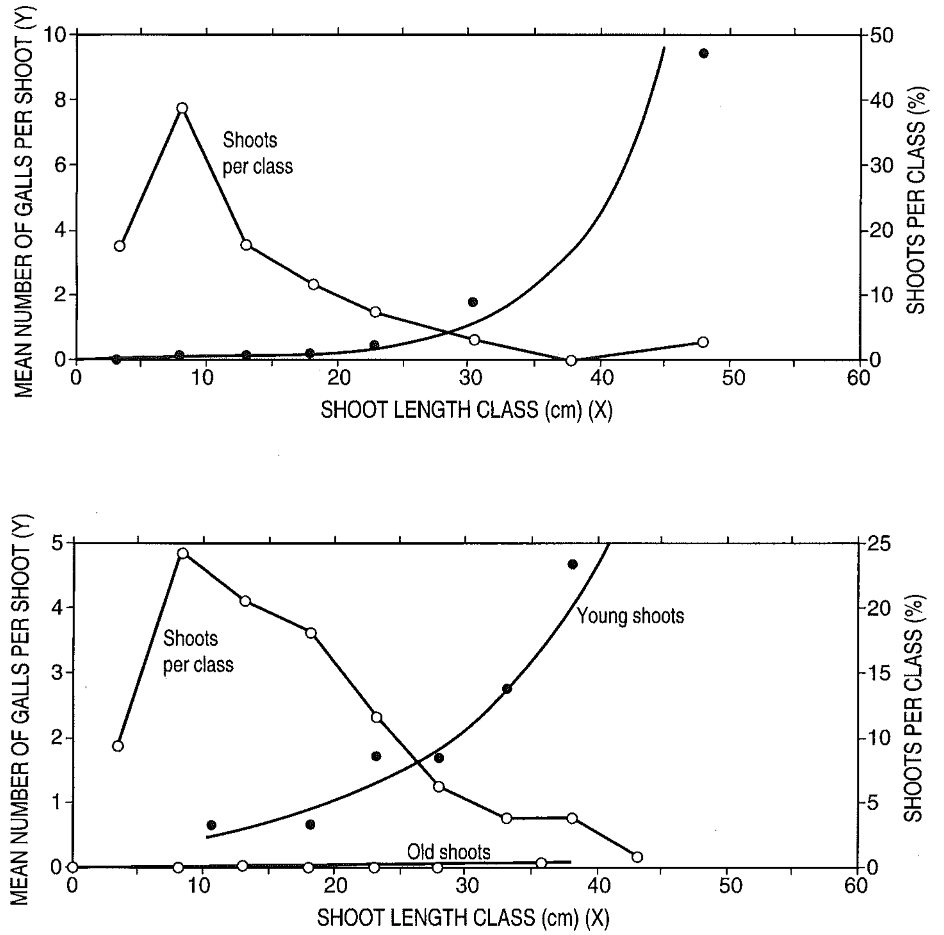

Fig. 5. Distribution of shoots and mean number of galls per shoot in relation to shoot-length class in Tree 3 (above) and Tree 4 (below), both relatively young trees with mostly actively growing upright shoots (*Ua* type). Based on 262 shoots and 114 galls and 7 shoot-length classes for Tree 3; 310 shoots, 160 galls and 6 shoot-length classes for both active (*Ua* = young shoots) and dormant shoot (*Ud* = old shoots) types in Tree 4.

Overall, nonsignificant patterns of attack in relation to shoot length in general have been identified in Trees 1 and 5, but where active shoots of the *Ua*-type predominate, significant and positive relationships prevail, as in Trees 2, 3, 4, and 5. Shoots are utilized by gall-inducing larvae so long as there is active meristematic development, independent of shoot length, but longer active shoots with more resources available (cf. Fig. 3) support more larvae and galls.

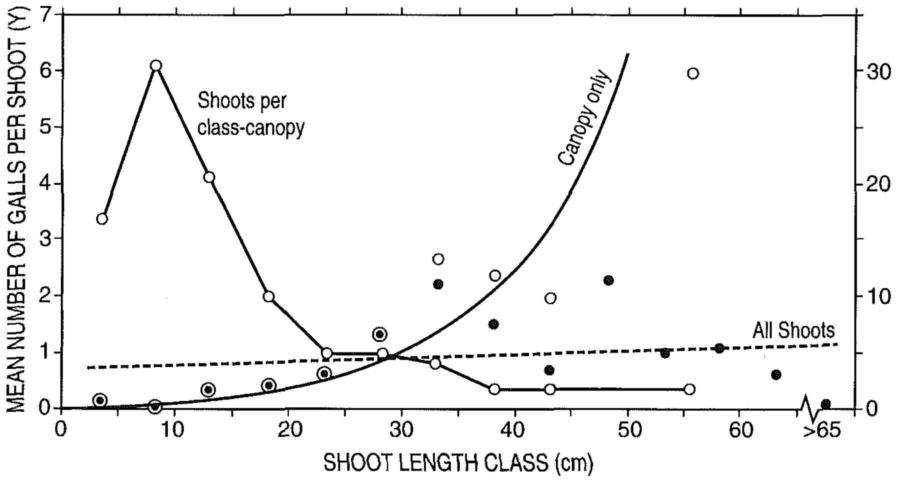

Fig. 6. The distribution of shoots and mean number of galls per shoot in relation to shoot-length class in Tree 5, a large pruned tree with basal shoots (see Fig. 2). Based on 343 shoots, 169 galls, and 10 shoot-length classes for canopy shoots (large proportion of *Pa* shoots) and 14 classes for all shoots. Open circles are for canopy shoots, closed circles are for all shoots, with basal (*Ba*) shoots dominating in the 40+ cm classes. The reason for low attack on *Ba* shoots is not known, but female moths are likely to concentrate oviposition in the canopy.

DISCUSSION

Amblypalpis life history

The life history of the spindle-gall moth in Israel conforms with other gelechiid gall inducers, in the genus *Gnorimoschema*, from the north temperate region. Adults of this genus emerge in the fall and oviposit on old goldenrod plants (Asteraceae, genus *Solidago*). Eggs hatch the following spring and larvae initiate galls in young stems of goldenrod (Borror et al., 1992), which are similar in shape to *Amblypalpis* galls.

In general, members of the Gelechiidae are borers, miners, or leaf tiers or rollers, with only a few gall-inducing species. Apparently, the larvae of gall inducers have retained the more primitive habit of boring while also developing the ability to initiate gall formation. Final instar larvae in galls bore a hole in the gall wall (Fig. 1), eject frass through this hole, and spin silk to seal the tunnel (Lupo and Gerling, 1984). In other gall-inducing microlepidopteran species, derived from a general stem-boring stock, larvae keep a hole open in the gall throughout development, as in *Epiblema scudderiana* (Lepidoptera:Tortricidae; Miller, 1976; Martel, 1995). Thus, the behavior of *Amblypalpis* larvae is more derived than that of *Epiblema* species but still, no doubt represents a relatively primitive form of gall induction.

The gelechiid gall inducers do differ considerably in life cycle characteristics from most other gall-inducing groups studied mostly in north temperate climates: sawflies, gall wasps, gall midges, and fruit flies. In these groups oviposition is usually synchronized with rapidly growing shoots and eggs are laid directly into immature plant tissue, or close to such tissue, in which case larvae crawl to a site and bore into a module (e.g., some Cecidomyiidae). Thus, oviposition by *Amblypalpis* onto tree bark in November and December, with eggs in diapause for 3–4 months, is very different from most galling taxa. This results in females unable to select high-quality sites for larval feeding, and larvae must forage independently, in many cases up to 20 or 30 cm. There is no ovipositional preference and larval performance linkage as seen in some other gall-inducing insects (e.g., Craig et al., 1989).

The long oviposition period of almost 3 months when adults are emerging, with placement of eggs in cracks in bark over many parts of a canopy, probably contributes to the prolonged emergence time of larvae from March into May. Hatching time is given as March and April by Lupo and Gerling (1984), but in mid-May 1998, new galls had been initiated very recently. This prolonged period of gall initiation is considerably longer than in other gall-inducing groups in general, and appears to have adaptive value in enabling exploitation of the phenologically diverse array of active meristems provided by host tree individuals and populations. We would predict more protracted phenologies in other warm temperate and tropical climates relative to those in north temperate zones.

The plant vigor hypothesis

The results of this study are largely consistent with the plant vigor hypothesis. Larvae initiated galls near active meristems, and the more meristems on a shoot, associated with shoot length, the more galls were formed. However, shoot-length class was not necessarily an effective indicator of galling activity. This was particularly apparent when many short and vigorous shoots were present, as in Tree 1, and when basal shoots (*Ba* type) were present, as in Tree 5. Why the most vigorous shoots, of the *Ba* type, were not more heavily attacked is unclear and needs more study, but it is likely that fewer eggs are laid close to the ground than in the canopy, and it is possible that *Ba* shoots are attacked only by larvae that fall from the tree crown. Also, growth of gall tissue may overwhelm some larvae, as noted by Lupo and Gerling (1984), diminishing the observed population.

The heterogeneity of shoot development in space and time made the test of the plant vigor hypothesis more precarious because after apical growth had ceased later in the dry season, the critical character of meristematic activity would not be evident, and patterns in galling relative to shoot-length class would have been inconsistent, as we saw in Trees 1 and 5 when compared to Trees 2, 3, and 4. This situation contrasts with north temperate systems, where shoot length is normally a good indicator of relative vigor no matter when in the season measurements are made, unless gall induction reduces shoot elongation (shoot growth is stunted by galling in some cases (e.g., Caouette and Price, 1989)). For example, for a bud-galling sawfly, attack correlated positively with shoot length well after the growing season in the following spring (Price et al., 1987a,b).

Extension of studies on plant vigor and herbivore attack into the warm temperate and tropical latitudes is needed to expand the comparative basis for testing the plant vigor hypothesis. This study emphasizes the need for investigation at the time of herbivore attack or immediately after attack to capture the nature of the relationship. In fact, we had anticipated a lack of any vigor-related attack because females laid eggs away from sites of gall induction and could not select high-quality sites for larval utilization, and casual observations had suggested a lack of a significant relationship between shoot length and probability of attack, as illustrated in Tree 1. Of course fires at the lower latitudes will frequently result in a synchronous flush of new growth, in which patterns of herbivore attack in relation to plant vigor are more readily detected (e.g., Prada et al., 1995; Vieira et al., 1996; Seyffarth et al., 1996). But failing this opportunity the need is for longer-term studies that record fully the phenology of shoot growth on different types of shoots and the phenology of herbivore attack, a topic that is gaining increasing attention in the literature, even for north temperate systems (e.g., Hunter, 1990, 1992a,b; Senn et al., 1992; Hunter et al., 1997). In addition, valuable additions to the understanding of this species would derive from studies on larval performance (survival, weight, etc.) on the different shoots utilized. We did not investigate larval performance in the present study.

The considerable complexity of resources for *Amblypalpis* larvae, contributed by different shoot types, phenology, and growth rates, results in an apparent gross underutilization of resources, for many shoots are not attacked. This underutilization results clearly from the heterogeneity of available resources, a host plant effect, rather than from population regulation by natural enemies. Once in a stem, survival of larvae is remarkably high, based on our studies at the study site, and a high proportion of galls in the 1997 generation had adult emergence holes. Lupo and Gerling (1984) reported emergence of adults at coastal sites in Tel Aviv, for 1976, in the range of 36–54%, very high values compared to general survivorship among insect herbivores (cf. Cornell and Hawkins, 1995; Price, 1997).

An unresolved issue is the extent to which the trees in our study represent a natural system or an urbanized environment. In either case the results are interesting, for we need to understand the ecology of each. *Tamarix* was introduced to coastal Israel, to stabilize sand, from the lower Jordan River and Dead Sea area, part of its natural range. Coastal populations are commonly attacked heavily by the spindle-gall moth, but exist at much lower populations along the Dead Sea (personal observations). Hence, the study area was situated in a vegetation heavily influenced by humans. The urban setting may also have added heterogeneity, although the trees appeared to be equivalent to those in adjacent sites with no landscaping. Further studies would help to define whether the heterogeneity we describe is common in wilder populations along the coast and along the Jordan River and Dead Sea.

More research is needed in warm temperate climates to test hypotheses on plant and herbivore interactions developed largely from studies in north temperate climates (cf. Price, 1997). This study indicates that such tests may be complicated by the greater heterogeneity of plant resources allowed by longer growing seasons and grossly asynchronous development of modules within individual host plants. However, in the particular case of the plant vigor hypothesis developed on the basis of studies in north temperate climates, the results reported here are consistent with the hypothesis.

An excellent opportunity for comparative studies of gall-inducing insects at the same latitudes is provided by the extensive research on aphid-induced galls on *Pistacia* trees in Israel by Wool and associates (e.g., Wool, 1990, 1995; Burstein and Wool, 1993; Burstein et al., 1994; Wool and Ben-Zvi, 1998; Wool and Inbar, 1998; Wool and Bogan, 1999). While these studies have not focused on shoot length and probability of attack by gall-inducing aphids, their results are provocative. On the one hand, after a burn, many more trees were attacked by *Baizongia pistaciae* (L.) (Homoptera: Pemphigidae) than unburned control trees (Wool and Inbar, 1998), suggesting a positive response to rapidly growing resprouting trees. On the other hand, *Smynthurodes betae* Westw., in the same aphid family, showed no linkage between female preference and nymphal performance (Burstein and Wool, 1993).

Additional studies by Whitham (e.g., 1978, 1979, 1980) on *Pemphigus betae* (Doane) showed strong female preference for the largest leaves of host trees, and a strong linkage to nymphal performance.

An interesting approach to comparative studies on gall-inducing insects would be to employ as a basis a measure of module size (leaf, shoot, bud) and/or host plant age. Then, responses of attack by gall inducers and performance (survival of nymphs or larvae) could be estimated in relation to host plant module and/or age classes. We predict that some broad patterns would emerge, providing plant architecture is understood, and exceptional cases may then be explored for rational explanations. With such an approach a synthesis of gall-inducing insect ecology may be achieved, forming the basis for a theory on plant–herbivore interactions involving such species.

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