

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.de/flora

Spiny east Mediterranean plant species flower later and in a drier season than non-spiny species

Michal Ronel¹, Gidi Néeman, Simcha Lev-yadun*

Department of Science Education – Biology, Faculty of Science and Science Education, University of Haifa – Oranim, Tivon 36006, Israel

ARTICLE INFO

Article history:

Received 20 January 2009

Accepted 13 May 2009

Keywords:

Defense
Evolution
Flowering
Herbivory
Phenology
Spines

ABSTRACT

We compared the flowering phenology of spiny and non-spiny native species belonging to three families (Asteraceae, Fabaceae and Lamiaceae), which include the highest number of spiny species in the flora of Israel. We found that the peak of flowering (when the highest number of species flowered) was 4–8 weeks later for spiny species than for non-spiny species. The flowering peak of non-spiny species was in late March, while that of spiny species was at the beginning of May. The seasonal shift in flowering time from the main season, when most Mediterranean plants bloom, to the end of the flowering season, when fewer species bloom, might be the evolutionary result of a change in phenology reducing the competition for pollinators. Our results clearly indicate that spinescence of plants in the semi-arid east Mediterranean region is associated with a delayed flowering season at the beginning of the dry summer when most of the herbaceous vegetation is already dry. During this season, mammalian grazers consume any edible herbaceous vegetation, selecting for late flowering species that allocate more resources for anti-herbivore defenses than early flowering species. There is a well-known global geographical trend where the occurrence of spiny plants is higher in arid regions than in humid ones. In parallel to the global trend, we show a seasonal one, that non-spiny plants grow and flower in the spring, which is the main flowering season in the Mediterranean basin, while spiny plants flower later, in the hot and dry summer. Under the current trend of global warming, there are prospects of future increase in the dominance of spiny species in the Mediterranean region.

© 2009 Elsevier GmbH. All rights reserved.

Introduction

Most mammalian herbivores utilize the aboveground parts of plants as their food (Crawley, 1983). Thus, there is a permanent evolutionary arms race between the plants and their herbivores, in which, on an evolutionary time scale, plants acquire better defenses and herbivores partly or fully overcome them (Cornell and Hawkins, 2003). Spines, thorns and prickles are well known as physical protection against herbivory (e.g., Cash and Fulbright, 2005; Cooper and Owen-Smith, 1986; Grubb, 1992; Gowda, 1996; Janzen, 1986; Janzen and Martin, 1982; Myers and Bazely, 1991; Rebollo et al., 2002) because they can wound mouth parts and digestive systems (Janzen and Martin, 1982; Janzen, 1986) as well as other body parts of the herbivores. In addition, spines inject pathogenic bacteria and fungi into large herbivores (Halpern et al., 2007a, 2007b; Lev-Yadun and Halpern, 2008).

English botanical usage distinguishes between a prickle (a sharp emergence from the cortex), a spine (a sharp part of a

leaf) and a thorn (a sharp branch). We will use the specific term whenever possible and mention spines when generally discussing defense by sharp plant organs because spines are the most common sharp organ in the taxa discussed here. Being spiny not only slows the rate of feeding within the canopy of the individual plant by reducing the size of ingested plant parts in various large herbivores (e.g., Cooper and Owen-Smith, 1986; Wilson and Kerley, 2003), but also gives a considerable overall advantage to such plants over non-defended ones (Stapley, 1998; Rebollo et al., 2002).

From ecological and evolutionary points of view, spinescence should increase as a response to continuous herbivory by large animals (Givnish et al., 1994; Grubb, 1992; Janzen, 1986; Zohary, 1983). Moreover, even during the lifetime of an individual plant, spinescence may increase as an induced defense mechanism following browsing (e.g., Fornara and Du Toit, 2007; Gómez and Zamora, 2002; Goheen et al., 2007; Huntzinger et al., 2004; Milewski et al., 1991; Perevolotsky and Haimov, 1991; Young et al., 2003). The evolution of plants in arid regions is under constant pressure of natural herbivory: the millennia-long history of intensive grazing by goat, sheep, cattle, horses and donkeys in the Near East (e.g., Zohary, 1983) and the long, pre-agricultural history of grazing by the various mammalian herbivores that

* Corresponding author.

E-mail address: levyadun@research.haifa.ac.il (S. Lev-yadun).

¹ In partial fulfillment of requirements for the degree of Ph.D.

existed in the land during the Pleistocene (e.g., Bar-Oz, 2004; Davis, 1987; Steiner, 2005; Tchernov, 1979) selected for plants that are better protected from grazing and resulted in an increase in their proportion in the plant populations (Noy-Meir et al., 1989; Perevolotsky, 1994; Perevolotsky and Seligman, 1998; Seligman et al., 1959; Zohary, 1983). Fieldwork in an ecosystem that has a millennia-long history of large-scale grazing, such as in Israel, clearly and “sharply” indicates the ecological benefit of being spiny. A continuous blanket of spiny shrubs such as *Sarcopoterium spinosum*, *Calicotome villosa* and many types of thistles covers large tracts of the land, and many other areas are rich with dozens of spiny plant species that dominate the vegetation (Shmida, 1981; Zohary, 1962, 1983). This dominance clearly indicates the adaptive value of being spiny under high grazing pressure.

Grubb (1992), who reviewed many previous studies, concluded that spines are a common defense in arid regions. Later, Lev-Yadun and Néeman (2004) showed that there are several common desert plants, which contrary to the general plant phenology in this region, are conspicuously green during summer, when all the surroundings are yellow. In such conditions, green was proposed to be conspicuous and contrasts with the background, as do yellow, red and black colors in greener ecosystems. These summer-green plants are poisonous or thorny as a protection against herbivory. Lev-Yadun and Néeman (2004) proposed that during summer in the dry desert, when most other plants are dry, a vivid green color can be aposematic, although olfactory aposematism (e.g., Eisner and Grant, 1981; Launchbaugh and Provenza, 1993; Lev-Yadun et al., 2009) may also be involved.

The typical Mediterranean summer is hot, dry and long, presenting a significant physiological challenge to plants. As a result, early spring is the peak flowering season in the Mediterranean basin (Bosch et al., 1997; Petanidou et al., 1995). This makes spring a wonderful season for nature lovers, but a harsh one for flowers which must compete for their pollinators. Competition for pollinators has been well documented and reviewed (Mitchell et al., 2009), and several hypotheses and models have been proposed about the outcome of competition for pollinators. It may lead to the rapid elimination of a minority species (Levin and Anderson, 1970), to the evolution of autogamy (Levin, 1972), to specialization to different pollinating agents (Grant and Grant, 1965), or it may influence the flowering time of some species (Mosquin, 1971). Seasonal segregation in blooming time of related plant species, or plants that belong to the same pollination guild, is well documented in many biomes – arctic (e.g., Hocking, 1968), temperate (e.g., Heinrich, 1975; Lack, 1976; Mosquin, 1971) and neotropical (e.g., Frankie et al., 1974; Feinsinger, 1978; Heithaus, 1974). It has been interpreted as an evolutionary result of competition for pollination, and in some cases competition for pollinator was also experimentally proven to be the evolutionary driver (Waser, 1978; Pleasants, 1980). Therefore, we assume that late flowering species of the Israeli flora may also represent such a case. However, in addition to the risk of drought, late flowering species are also exposed to increased risk of large herbivores (e.g., Gutman and Seligman, 1979; Seligman et al., 1959; Zohary, 1962, 1983). An improved defense against such herbivores, for instance by a spiny morphology should confer advantages for such plants. We examined the hypothesis that in the semi-arid flora of Israel non-spiny plants flower in spring, while spiny plants flower later, at the beginning of summer.

Materials and methods

As part of a broader study on the evolution of plant protection by spines (e.g., Halpern et al., 2007a, 2007b; Lev-Yadun, 2001,

2003a, 2003b, 2006, 2009a, b, c; Lev-Yadun and Néeman, 2004, 2006; Lev-Yadun and Gould, 2008; Lev-Yadun and Halpern, 2008; Nassar and Lev-Yadun, 2009; Ronel and Lev-Yadun, 2009; Ronel et al., 2007, 2009) we studied the flowering phenology of spiny and non-spiny species of the Asteraceae, Fabaceae and Lamiaceae in Israel. These families include the largest number of spiny species in the local flora.

To further understand the issue of summer conspicuousness of well-defended plants in the Mediterranean flora, we examined the possibility that the peak of the flowering season of spiny and thorny plants is in the beginning of the dry summer, later than that of non-spiny plants which flower during spring time. From the analytical flora (Feinbrun-Dothan and Danin, 1991) we compiled data about the flowering season (given in the flora in months) of all native species of the three families that include the largest number of spiny species: Asteraceae with 92 spiny out of 287 species (e.g., Ronel et al., 2009), Fabaceae with 28 spiny out of 298 species, and Lamiaceae with 13 spiny out of 227 species. For each species we tabulated the months in which it was reported flowering and counted the number of non-spiny and spiny species that flowered in each month (Appendix 2). We excluded from the analysis domesticated plants and species that arrived in Israel in the last 100 years.

We used the median of the distribution of the monthly number of flowering species as an indicator for the peak flowering season for each group. We used χ^2 tests to examine the relation between the total number of spiny and non-spiny species of each family and of all families together, that flower in each month.

Results

The Asteraceae, Fabaceae and Lamiaceae of the Israeli flora include many spiny species (Appendix 1). The 195 non-spiny species of the Asteraceae have their flowering peak at the beginning of April, while the 92 spiny species have it at mid-June (Fig. 1A, Appendix 1). The 270 non-spiny species of the Fabaceae have their flowering peak at mid-April, while the 28 spiny species have it at mid-May (Fig. 1B, Appendix 1). The 114 non-spiny species of the Lamiaceae have their peak of flowering at the beginning of May, while the 13 spiny species have it at mid-May (Fig. 1C, Appendix 1). A comparison of all 133 spiny species of these families with all 589 non-spiny species of these families showed that the peak in flowering of the spiny species is at the beginning of May while that of the non-spiny species is in late March (Fig. 1D, Appendix 1). The distribution of the number of non-spiny and spiny species that flowered in the various months, differed significantly for the Asteraceae, Fabaceae and for all families together, but not for the Lamiaceae Table 1.

Discussion

The Mediterranean climate is characterized by a short, mild and wet winter and a contrasting long, dry and hot summer (Zohary, 1973). Lush green herbaceous plants dominate the Mediterranean landscape during winter and spring. Zohary (1962) compiled the flowering time of the whole flora of Israel and found that the peak of flowering occurs in April, when about 1600 species flower simultaneously. Hot and dry spells characterize the late spring in Israel and under these extreme conditions the green landscape changes its color to yellow within a couple of days. Under heavy grazing, a considerable part of the grass disappears shortly after the end of the rainy season (Gutman and Seligman, 1979; Henkin et al., 1998; Seligman et al., 1959). Thus, delaying growth and flowering phenology from April to May

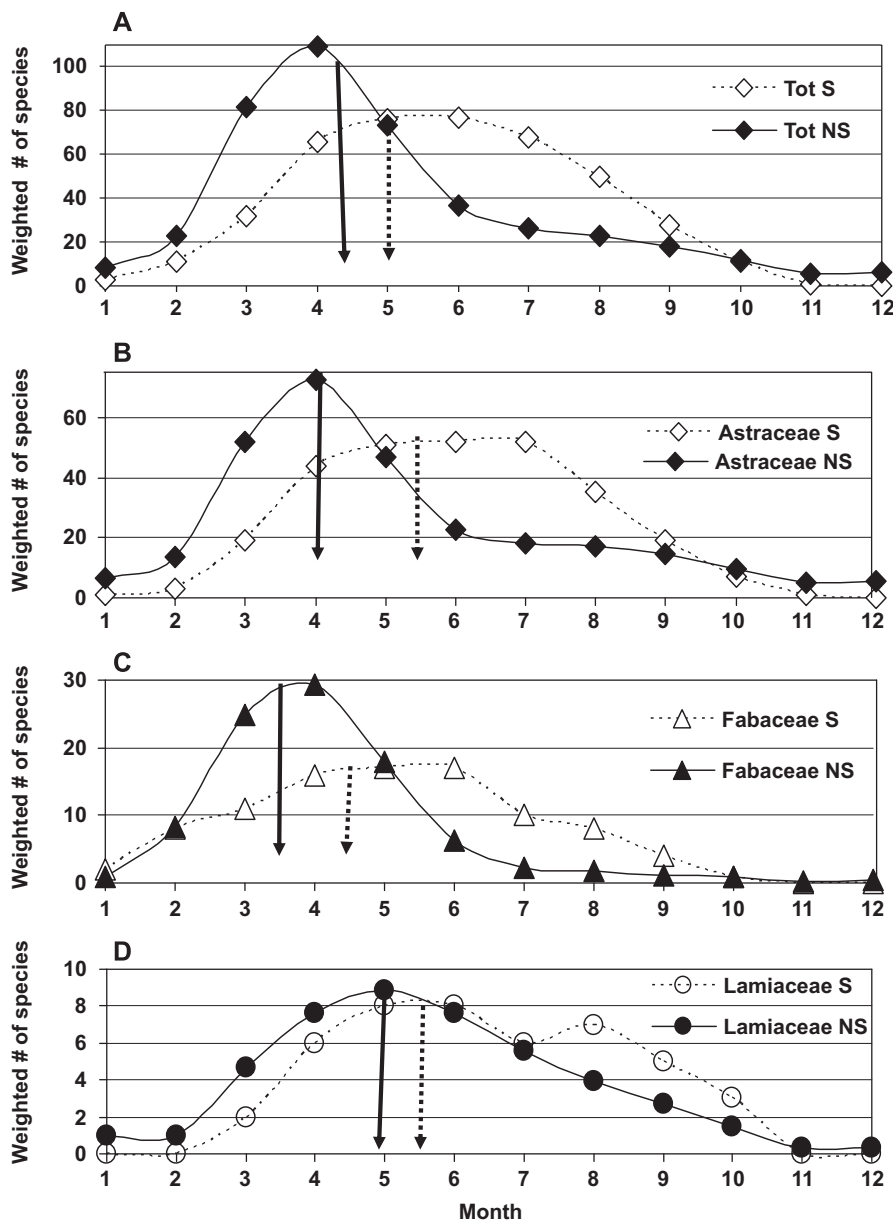


Fig. 1. Distribution by months of the number of flowering spiny (S) and non-spiny (NS) species in all families together (A), Asteraceae (B), Fabaceae (C), and Lamiaceae (D). Solid line arrows indicate the median of non-spiny and broken line arrows indicate the median of spiny species.

Table 1

The number of spiny and non-spiny species in the Asteraceae, Fabaceae and Lamiaceae of the Israeli flora, and results of χ^2 testing the relations between the total number of spiny and non-spiny species that flower in each month separately for each family and of all families together.

Family	Non-spiny (N)	Spiny (N)	Total (N)	Chi-Square	df	P
Asteraceae	612	284	896	103.61	11	<0.001
Fabaceae	802	94	896	64.05	11	<0.001
Lamiaceae	403	45	448	9.62	11	0.5650
All families	1817	423	2240	164.95	11	<0.001

or June, exposes the plants to severe drought, and increases grazing risk when the group defense of the lush green vegetation has already disappeared.

Production of spines is a common type of physical protection against vertebrate herbivores in species of the Asteraceae, Fabaceae and Lamiaceae, and these families contain the largest

number of spiny species in the flora of Israel. Being spiny defends plants from mammalian herbivores (Cooper and Owen-Smith, 1986; Grubb, 1992; Janzen, 1986). We found a clear phenological difference in flowering time between spiny and non-spiny plant species in these three families (Fig. 1), which might be a consequence of a long and repetitive evolutionary process. The data clearly indicate that the physical defense of the plants by spines is associated with a flowering season delayed to the dry summer, a period with a much greater impact of mammalian grazers and drought stress. As the summer progresses, in many areas of the Near East non-spiny and non-poisonous plants gradually disappear as the outcome of intensive grazing activity (Gutman et al., 1990; Noy-Meir, 1990; Seligman et al., 1959). Even in spring (March–April) and throughout the summer, spiny thistles such as *Echinops viscosus*, *Notobasis syriaca*, *Silybum marianum*, *Onopordum* sp., *Centaurea* sp., *Carthamus* sp. and *Scolymus maculatus* dominate many areas that are under intensive cattle and sheep grazing, when the favored edible plants can

hardly be seen. The published stocking rates of sheep, goat and cattle in studied rangelands are not very high because studies of modern range management include supplemental feeding and high economic returns. However, traditional grazing does not include supplemental feeding and its stocking rate is much higher, with the consequent higher impact on the vegetation. We saw such higher levels of grazing impact in areas under traditional grazing regime in the Palestinian Authority, southern Lebanon, the northern Sinai (Egypt) and the Bedouin rangelands in the Arad region (Israel). Therefore, the published values of remaining plant biomass and taxa in controlled experiments (e.g., Gutman and Seligman, 1979; Gutman et al., 1990, 1999; Noy-Meir, 1990; Seligman et al., 1959) represent only moderate levels of grazing.

While the role of spines and thorns in defense from large herbivores is clear (e.g., Cooper and Owen-Smith, 1986; Grubb, 1992; Janzen, 1986; Nobel, 1994; Rebollo et al., 2002; Young, 1987; Zohary, 1983), they may also serve physiological functions, such as protecting from heating by the sun, lowering photoinhibition and insulation from low temperatures (Gibson and Nobel, 1986; Nobel, 1994). We cannot exclude various physiological gains as part of the function of spines in some of the species discussed here that have a dense cover of spines.

Spiny and thorny plants are more common in arid regions of the world than in humid ones (Carlquist, 1974; Grubb, 1992; Milton, 1991; Parsons and Moldenke, 1975; Shmida, 1981). We show here a parallel seasonal trend in the flora of Israel, in which the functional group of spiny species grows and flowers later in the season when the weather is warm and dry, while the non-spiny species grow and flower earlier in the spring under more favorable conditions. These trends are in accordance with the general pattern of stronger anti-herbivory defense found in slow-growing plants in habitats with limited resources (Coley et al., 1985; McKey et al., 1978).

The shift in flowering of spiny plants towards the summer that we describe may initially result from competition for pollinators. Similar shifts in flowering season are well known in various ecosystems (Mitchell et al., 2009 and citations therein). We assume that late flowering spiny species of the Israeli flora may also represent such a case. There are two alternative scenarios that could have led to the association of defense by spines and summer flowering: (1) the later flowering exposed the plants to an increased risk of grazing, and this pressure selected for better defense, or (2) plants that were better defended could evolve towards later flowering because they were damaged less by the herbivores. Without a thorough comparative study of the genetic basis for both early versus late flowering, and defense by spines versus the lack of such defense, in several pairs of species per families discussed (Asteraceae, Fabaceae and Lamiaceae), it is practically impossible to determine the evolutionary route of the seasonal shift.

Plants have to compromise between allocation to growth or defense (Herms and Mattson, 1992). The death of many young annual plants within dense cohorts during the growing season is a well-known phenomenon (Harper, 1977). East Mediterranean plants, which grow in dense populations in winter and spring, suffer from strong intra- and inter-specific competition, and consequently many of them die (e.g., Gutman et al., 1999; Gutman and Seligman, 1979; Noy-Meir et al., 1991). Under such conditions, winter and early spring plants have to invest more in vegetative growth to withstand competition than to defense (e.g., Grime, 2001; Herms and Mattson, 1992; Kadmon and Shmida, 1990), especially when they are protected by lush vegetation (a vegetative parallel to mast seeding or animal schooling). In summer, the highly edible

green herbaceous plants are much less abundant (Gutman et al., 1990; Gutman and Seligman, 1979; Noy-Meir et al., 1991; Noy-Meir, 2001; Seligman et al., 1959) and the group defense of lush green herbaceous plants practically disappears. Thus, to survive, plants have to allocate more to defense. This greater need for defense in summer in the Eastern Mediterranean also accords with the concept of high apparency associated with higher investment in defense *sensu* Feeny (1976) and Euler and Baldwin (1996). It is believed that the world stays green because many plants evolved to be inadequate for herbivores (White, 2005), usually because of low nutritional (nitrogen) value. Here we demonstrate that green plants in the dry Mediterranean summer also became inadequate food for herbivores because of mechanical defense by spines and thorns. Moreover, under the current trend of global warming, there are prospects of a future increase in the dominance of spiny species in the Mediterranean, a process already evident by cacti invasion in Europe (e.g., Essl and Kobler, 2009).

Acknowledgement

We thank two anonymous reviewers for their constructive comments.

Appendix 1. The spiny species included in this study by their families

Asteraceae ($n=92$): *Phagnalon barbeyanum*, *Iphiona mucronata*, *I. scabra*, *Anvillea garcinii*, *Pallenis spinosa*, *Xanthium spinosum*, *X. stromarium*, *Gundelia tournefortii*, *Echinops viscosus*, *E. gaillardotii*, *E. adenocaulos*, *E. glaberrimus*, *E. philistaeus*, *E. polyceras*, *Acantholepis orientalis*, *Cardopatum corymbosum*, *Siebera pungens*, *Carlina lanata*, *C. racemosa*, *C. curetum*, *C. hispanica*, *Atractylis comosa*, *A. prolifera*, *A. cancellata*, *A. carduus*, *A. serratulooides*, *A. phaeolepis*, *Cousinia moabitica*, *C. postiana*, *C. libanotica*, *C. hermonis*, *Jurinea staezelinae*, *Carduus argentatus*, *C. australis*, *C. getulus*, *Notobasis syriaca*, *Cirsium phyllocephalum*, *C. gaillardotii*, *C. alatum*, *Picnomon acarna*, *Ptilostemon chamaepeuce*, *P. diacanthum*, *Cynara syriaca*, *Silybum marianum*, *Onopordum cynarocephalum*, *O. blancheanum*, *O. carduiforme*, *O. macrocephalum*, *O. ambiguum*, *O. anisacanthum*, *O. alexandrinum*, *O. transjordanicum*, *O. jordanicolum*, *O. palaestinum*, *Serratula cerinthifolia*, *S. pusilla*, *Aegialophila pumilio*, *Centaurea crocodylium*, *C. ammocyanus*, *C. balsamita*, *C. dumulosa*, *C. damascena*, *C. rigida*, *C. behen*, *C. ascalonica*, *C. drabifolia*, *C. onopordifolia*, *C. solstitialis*, *C. verutum*, *C. eryngioides*, *C. speciosa*, *C. sinaica*, *C. lanulata*, *C. aegyptiaca*, *C. scoparia*, *C. hyalolepis*, *C. procurrens*, *C. iberica*, *C. pallescens*, *Carthamus persicus*, *C. nitidus*, *C. glaucus*, *C. tenuis*, *Carduncellus eriocephalus*, *Cnicus benedictus*, *Scolymus maculatus*, *S. hispanicus*, *Helminthotheca echioides*, *Launaea spinosa*, *Lactuca orientalis*, *L. saligna*, *L. aculeata*.

Fabaceae ($n=28$): *Crotalaria aegyptiaca*, *Calicotome villosa*, *Genista libanotica*, *G. fasselata*, *Astragalus spinosus*, *A. coluteoides*, *A. angustifolius*, *A. dactylocarpus*, *A. sieberi*, *A. deinacanthus*, *A. gummifer*, *A. cephalotes*, *A. echinus*, *A. cruentiflorus*, *A. bethlehemiticus*, *A. sparsus*, *A. fruticosus*, *Onobrychis cornuta*, *O. caput-galli*, *O. squarrosa*, *O. crista-galli*, *O. ptolemaica*, *O. wettsteinii*, *O. montana*, *O. kotschyana*, *Alhagi graecorum*, *Ononis spinosa*, *Trifolium scabrum*.

Lamiaceae ($n=13$): *Teucrium spinosum*, *T. leucocladum*, *Marrubium alysson*, *Sideritis perfoliata*, *S. pullulans*, *Moluccella spinosa*, *Ballota saxatilis*, *Stachys cretica*, *S. spectabilis*, *S. ehrenbergii*, *Salvia spinosa*, *S. palaestina*, *S. samuelssonii*.

Appendix 2

The number of spiny and non-spiny species of the Asteraceae, Fabaceae and Lamiaceae in the flora of Israel that flower in each month.

See Table A1.

Table A1

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Asteraceae												
Spiny	1	3	19	44	51	52	52	35	19	7	1	0
Non-spiny	14	29	112	156	101	49	39	37	31	21	11	12
Fabaceae												
Spiny	2	8	11	16	17	17	10	8	4	1	0	0
Non-spiny	7	70	212	250	152	53	20	16	10	7	2	3
Lamiaceae												
Spiny	0	0	2	6	8	8	6	7	5	3	0	0
Non-spiny	9	20	42	68	79	68	50	35	24	13	3	3
All families												
Spiny	3	11	32	66	76	77	68	50	28	11	1	0
Non-spiny	30	119	366	474	332	170	109	88	65	41	15	18

References

- Bar-Oz, G., 2004. Epipalaeolithic Subsistence Strategies in the Levant: A Zooarchaeological Perspective. The American School of Prehistoric Research (ASPR) Monograph Series, Brill Academic Publishers INC., Boston.
- Bosch, J., Retana, J., Cerd, X., 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* 109, 583–591.
- Carlquist, S., 1974. Island Biology. Columbia University Press, New York.
- Cash, V.W., Fulbright, T.E., 2005. Nutrient enrichment, tannins, and thorns: effects on browsing of shrub seedlings. *J. Wildl. Manage.* 69, 782–793.
- Coley, P.D., Bryant, J.P., Chapin III, F.S., 1985. Resource availability and plant antiherbivore defense. *Science* 230, 895–899.
- Cooper, S.M., Owen-Smith, N., 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68, 446–455.
- Cornell, H.V., Hawkins, B.A., 2003. Herbivore responses to plant secondary compounds: a test of phytochemical coevolution theory. *Am. Nat.* 161, 507–522.
- Crawley, M.J., 1983. *Herbivory. The Dynamics of Animal-Plant Interactions.* Blackwell, Oxford.
- Davis, S.J.M., 1987. *The Archaeology of Animals.* Yale University Press, New Haven.
- Eisner, T., Grant, R.P., 1981. Toxicity, odor aversion, and "olfactory aposematism". *Science* 213, 476.
- Essl, F., Kobler, J., 2009. Spiny invaders – patterns and determinants of cacti invasion in Europe. *Flora* 204, 485–494.
- Euler, M., Baldwin, I.T., 1996. The chemistry of defense and apparency in the corollas of *Nicotiana attenuata*. *Oecologia* 107, 102–112.
- Feeny, P., 1976. Plant apparency and chemical defense. *Recent Adv. Phytochem.* 10, 1–40.
- Feinbrun-Dothan, N., Danin, A., 1991. *Analytical Flora of Eretz-Israel.* Cana Publishing House Ltd., Jerusalem (in Hebrew).
- Feinsinger, P., 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol. Monogr.* 48, 269–287.
- Fornara, D.A., Du Toit, J.T., 2007. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88, 200–209.
- Frankie, G.W., Baker, H.G., Opler, P.A., 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62, 881–919.
- Gibson, A.C., Nobel, P.S., 1986. *The Cactus Primer.* Harvard University Press, Cambridge.
- Givnish, T.J., Sytsma, K.J., Smith, J.F., Hahn, W.J., 1994. Thorn-like prickles and heterophylly in Cyanea: adaptations to extinct avian browsers on Hawaii? *Proc. Natl. Acad. Sci. USA* 91, 2810–2814.
- Goheen, J.R., Young, T.P., Keesing, F., Palmer, T.M., 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *J. Ecol.* 95, 129–138.
- Gómez, J.M., Zamora, R., 2002. Thorns as induced mechanical defense in a long-lived shrub (*Hormathophylla spinosa*, Cruciferae). *Ecology* 83, 885–890.
- Gowda, J.H., 1996. Spines of *Acacia tortilis*: what do they defend and how? *Oikos* 77, 279–284.
- Grant, V., Grant, K.A., 1965. *Flower Pollination in the Phlox Family.* Columbia University Press, New York.
- Grime, J.P., 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties,* second ed. John Wiley & Sons, Chichester.
- Grubb, P.J., 1992. A positive distrust in simplicity – lessons from plant defences and from competition among plants and among animals. *J. Ecol.* 80, 585–610.
- Gutman, M., Seligman, N.G., 1979. Grazing management of Mediterranean foot-hill range in the upper Jordan River Valley. *J. Range Manage.* 32, 86–92.
- Gutman, M., Seligman, N.G., Noy-Meir, I., 1990. Herbage production of Mediterranean grassland under seasonal and yearlong grazing systems. *J. Range Manage.* 43, 64–68.
- Gutman, M., Holzer, Z., Baram, H., Noy-Meir, I., Seligman, N.G., 1999. Heavy stocking and early-season deferral of grazing on Mediterranean-type grassland. *J. Range Manage.* 52, 590–599.
- Halpern, M., Raats, D., Lev-Yadun, S., 2007a. Plant biological warfare: thorns inject pathogenic bacteria into herbivores. *Environ. Microbiol.* 9, 584–592.
- Halpern, M., Raats, D., Lev-Yadun, S., 2007b. The potential anti-herbivory role of microorganisms on plant thorns. *Plant Signaling Behav.* 2, 503–504.
- Harper, J.L., 1977. *Population Biology of Plants.* Academic Press, London.
- Heinrich, B., 1975. Bee flowers: a hypothesis on flower variety and blooming times. *Evolution* 29, 325–334.
- Heithaus, E.R., 1974. The role of plant pollinator interaction in determining community structure. *Ann. Mo. Bot. Gard.* 61, 675–691.
- Henkin, Z., Seligman, N.G., Kafkafi, U., Noy-Meir, I., 1998. 'Effective growing days': a simple predictive model of the response of herbaceous plant growth in a Mediterranean ecosystem to variation in rainfall and phosphorus availability. *J. Ecol.* 86, 137–148.
- Hermis, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* 67, 283–335.
- Hocking, B., 1968. Insect-flower associations in the high Arctic with special reference to nectar. *Oikos* 19, 359–388.
- Huntzinger, M., Karban, R., Young, T., Palmer, T.M., 2004. Relaxation of induced indirect defenses of acacias following exclusion of mammalian herbivores. *Ecology* 85, 609–614.
- Janzen, D.H., 1986. Chihuahuan Desert nopaleras: defaunated big mammal vegetation. *Annu. Rev. Ecol. Syst.* 17, 595–636.
- Janzen, D.H., Martin, P.S., 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215, 19–27.
- Kadmon, R., Shmida, A., 1990. Competition in a variable environment: an experimental study in a desert annual population. *Isr. J. Bot.* 39, 403–412.
- Lack, A., 1976. Competition for pollinators and evolution in *Centaurea*. *New Phytol.* 77, 787–792.
- Launchbaugh, K.L., Provenza, F.D., 1993. Can plants practice mimicry to avoid grazing by mammalian herbivores? *Oikos* 66, 501–504.
- Levin, D.A., 1972. Competition for pollinator service: a stimulus for the evolution of autogamy. *Evolution* 26, 668–669.
- Levin, D.A., Anderson, W.W., 1970. Competition for pollinators between simultaneously flowering species. *Am. Nat.* 104, 455–461.
- Lev-Yadun, S., 2001. Aposematic (warning) coloration associated with thorns in higher plants. *J. Theor. Biol.* 210, 385–388.
- Lev-Yadun, S., 2003a. Weapon (thorn) automimicry and mimicry of aposematic colorful thorns in plants. *J. Theor. Biol.* 224, 183–188.
- Lev-Yadun, S., 2003b. Why do some thorny plants resemble green zebras? *J. Theor. Biol.* 244, 483–489.
- Lev-Yadun, S., 2006. Defensive coloration in plants: a review of current ideas about anti-herbivore coloration strategies. In: Teixeira da Silva, J.A. (Ed.), *Floriculture, Ornamental and Plant Biotechnology: Advances and Topical Issues, Vol. IV.* Global Science Books, London, pp. 292–299.
- Lev-Yadun, S., 2009a. Aposematic (warning) coloration in plants. In: Baluska, F. (Ed.), *Plant-Environment Interactions. From Sensory Plant Biology to Active Plant Behavior.* Springer, Berlin, pp. 167–202.
- Lev-Yadun, S., 2009b. Müllerian and Batesian mimicry rings of white-variegated aposematic spiny and thorny plants: a hypothesis. *Isr. J. Plant Sci.* 57, 107–116.
- Lev-Yadun, S., 2009c. Müllerian mimicry in aposematic spiny plants. *Plant Signaling Behav.* 4, 482–483.
- Lev-Yadun, S., Gould, K.S., 2008. Role of anthocyanins in plant defense. In: Gould, K.S., Davies, K.M., Winefield, C. (Eds.), *Lifés Colorful Solutions: The Biosynthesis, Functions, and Applications of Anthocyanins.* Springer, Berlin, pp. 21–48.
- Lev-Yadun, S., Halpern, M., 2008. External and internal spines in plants insert pathogenic microorganisms into herbivore's tissues for defense. In: Van Dijk, T. (Ed.), *Microbial Ecology Research Trends.* Nova Scientific Publishers, New York, pp. 155–168.
- Lev-Yadun, S., Néeman, G., 2004. When may green plants be aposematic? *Biol. J. Linn. Soc.* 81, 413–416.
- Lev-Yadun, S., Néeman, G., 2006. Color changes in old aposematic thorns, spines, and prickles. *Isr. J. Plant Sci.* 54, 327–333.
- Lev-Yadun, S., Néeman, G., Shanas, U., 2009. A sheep in wolf's clothing: do carrion and dung odors of flowers not only attract pollinators but also deter herbivores? *BioEssays* 31, 84–88.
- McKey, D., Waterman, P.G., Mbi, C.N., Gartlan, J.S., Struhsaker, T.T., 1978. Phenolic content of vegetation in two African rain forests: ecological implications. *Science* 202, 61–64.
- Milewski, A.V., Young, T.P., Madden, D., 1991. Thorns as induced defenses: experimental evidence. *Oecologia* 86, 70–75.
- Milton, S.J., 1991. Plant spinescence in arid southern Africa: does moisture mediate selection by mammals? *Oecologia* 87, 279–287.
- Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M., Karron, J.D., 2009. New frontiers in competition for pollination. *Ann. Bot.* 103, 1403–1413.

- Mosquin, T., 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22, 398–402.
- Myers, J.H., Bazely, D., 1991. Thorns, spines, prickles, and hairs: are they stimulated by herbivory and do they deter herbivores?. In: Tallamy, D.W., Raupp, M.J. (Eds.), *Phytochemical Induction by Herbivores*. John Wiley & Sons, New York, pp. 325–344.
- Nassar, O., Lev-Yadun, S., 2009. How prickly is a prickly pear? *Isr. J. Plant Sci.* 57, 117–124.
- Nobel, P.S., 1994. In: *Remarkable Agaves and Cacti*. Oxford Univ. Press, New York.
- Noy-Meir, I., 1990. The effect of grazing on the abundance of wild wheat, barley and oat in Israel. *Biol. Conserv.* 51, 299–310.
- Noy-Meir, I., 2001. Ecology of wild emmer wheat in Mediterranean grasslands in Galilee. *Isr. J. Plant Sci.* 49, S43–S52.
- Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77, 290–310.
- Noy-Meir, I., Agami, M., Anikster, Y., 1991. Changes in the population density of wild emmer wheat (*Triticum turgidum* var. *dicoccoides*) in a Mediterranean grassland. *Isr. J. Bot.* 40, 385–395.
- Parsons, D.J., Moldenke, A.R., 1975. Convergence in vegetation structure along analogous climatic gradients in California and Chile. *Ecology* 56, 950–957.
- Perevolotsky, A., 1994. Tannins in Mediterranean woodland species: lack of response to browsing and thinning. *Oikos* 71, 333–340.
- Perevolotsky, A., Haimov, Y., 1991. Structural response of Mediterranean woodland species to disturbance: evidence of different defense strategies. *Isr. J. Bot.* 40, 305–313.
- Perevolotsky, A., Seligman, N., 1998. Role of grazing in Mediterranean rangeland ecosystems. Inversion of a paradigm. *BioScience* 48, 1007–1017.
- Petanidou, T., Ellis, W.N., Margaris, N.S., Vokou, D., 1995. Constraints on flowering phenology in a phryganic (East Mediterranean shrub) community. *Am. J. Bot.* 82, 607–620.
- Pleasants, J.M., 1980. Competition for bumblebee pollinators in rocky mountain plant communities. *Ecology* 61, 1446–1459.
- Rebollo, S., Milchunas, D.G., Noy-Meir, I., Chapman, P.L., 2002. The role of spiny plant refuge in structuring grazed shortgrass steppe plant communities. *Oikos* 98, 53–64.
- Ronel, M., Lev-Yadun, S., 2009. Spiny plants in the archaeological record of Israel. *J. Arid Environ.* 73, 754–761.
- Ronel, M., Malkiel, H., Lev-Yadun, S., 2007. Quantitative characterization of the thorn system of the common shrubs *Sarcopoterium spinosum* and *Calicotome villosa*. *Isr. J. Plant Sci.* 55, 63–72.
- Ronel, M., Khateeb, S., Lev-Yadun, S., 2009. Protective spiny modules in thistles of the Asteraceae in Israel. *J. Torrey Bot. Soc.* 136, 46–56.
- Seligman, N., Rosensaft, Z., Tadmor, N., Katzenelson, J., Naveh, Z., 1959. *Natural Pasture of Israel. Vegetation, Carrying Capacity and Improvement*. Sifriat Poalim, Merhavia in Hebrew.
- Shmida, A., 1981. Mediterranean vegetation in California and Israel: similarities and differences. *Isr. J. Bot.* 30, 105–123.
- Stapley, L., 1998. The interaction of thorns and symbiotic ants as an effective defence mechanism of swollen-thorn acacias. *Oecologia* 115, 401–405.
- Steiner, M.C., 2005. *The Faunas of Hayonim Cave (Israel): A 200,000-Year Record of Paleolithic Diet, Demography and Society*. Peabody Museum of Archaeology and Ethnology, Cambridge.
- Tchernov, E., 1979. Quaternary fauna. In: Horowitz, A. (Ed.), *The Quaternary of Israel*. Academic Press, New York, pp. 257–290.
- Waser, N.M., 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59, 934–944.
- White, T.C.R., 2005. In: *Why Does the World Stay Green? Nutrition and Survival of Plant-Eaters*. CSIRO Publishing, Collingwood.
- Wilson, S.L., Kerley, G.I.H., 2003. The effect of plant spinescence on the foraging efficiency of bushbuck and boergoats: browsers of similar body size. *J. Arid Environ.* 55, 150–158.
- Young, T.P., 1987. Increased thorn length in *Acacia depreanobium* – an induced response to browsing. *Oecologia* 71, 436–438.
- Young, T.P., Stanton, M.L., Christian, C.E., 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* 101, 171–179.
- Zohary, M., 1962. *Plant Life of Palestine, Israel and Jordan*. The Ronald Press Company, New York.
- Zohary, M., 1973. *Geobotanical Foundations of the Middle East*. G. Fischer, Stuttgart.
- Zohary, M., 1983. Man and vegetation in the Middle East. In: Holzner, W., Werger, M.J.A., Ikusima, I. (Eds.), *Man's Impact on Vegetation*. Dr W. Junk BV Publ., The Hague, pp. 287–295.