

This paper has been contributed in honor of Prof. Abraham Fahn on the occasion of his 90th birthday.

Color changes in old aposematic thorns, spines, and prickles

SIMCHA LEV-YADUN* AND GIDI NE'EMAN

*Department of Biology, Faculty of Science and Science Education,
University of Haifa—Oranim, Tiv'on 36006, Israel*

(Received 1 January 2007 and in revised form 25 January 2007)

ABSTRACT

Patterns of color changes of senescent colorful aposematic prickles, spines, and thorns are described. Color changes make the older prickles, spines, and thorns less conspicuous and they lose their aposematic character. The color changes and the aposematic character loss occur when the defended organs become less edible to large herbivores because of their increased size, mechanical rigidity, or chemical defense or when there is no need for defense. Reducing the cost of defense seems to be the reason for the ephemeral nature of conspicuousness of plant prickles, spines, and thorns.

Keywords: aposematic coloration, color change, defense, herbivory, prickles, spines, thorns

INTRODUCTION

Prickles, spines, and thorns are well known as mechanical protection against herbivory (Cooper and Owen-Smith, 1986; Janzen, 1986; Tomlinson, 1990; Grubb, 1992; Gowda, 1996). From both evolutionary and ecological points of view, thorniness increases in various ecosystems following lengthy exposure to herbivory by large animals (Zohary, 1983; Janzen, 1986; Givnish et al., 1994). Even during the lifetime of an individual plant, thorniness and spininess may increase following animal browsing as an induced defense (Milewski et al., 1991; Perevolotsky and Haimov, 1991; Young et al., 2003).

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 thorns when generally discussing defense by sharp plant organs.

Colors play an important role in plant/animal communication. The best-known communication system is color serving as an advertisement to attract various animals to flowers, which serve as their pollinators, hence as gene-dispersing agents as they transfer pollen among flowers (Darwin, 1877; Faegri and van der Pijl, 1979; Clegg and Durbin, 2003). The next-best-known system is fruit colors, which alert seed-dispersing frugivores to the ripening stage of the fruits (van der Pijl, 1982; Willson and Whelan, 1990). The third system is the phenomenon of fruit flags, namely, bright autumn leaves, which may signal to frugivores the existence of fruits (Stiles, 1982; Facelli, 1993), a debated hypothesis (Willson and Hoppes, 1986). The fourth system is found in carnivorous plants whose colorful patterns, in both visible and UV light, attract insects to their deadly traps

*Author to whom correspondence should be addressed
E-mails: levvadun@research.haifa.ac.il; gneeman@research.haifa.ac.il

(Joel et al., 1985; Moran et al., 1999). The fifth system is the bright colors of autumn leaves, found in many deciduous trees; recently it has been proposed that they signal the tree's vigor to its parasitic insects, especially aphids, and that this is a case of Zahavi's handicap principle operating in plants (Archetti, 2000; Hamilton and Brown, 2001; Hagen et al., 2003; Archetti and Brown, 2004; Schaefer and Wilkinson, 2004; Archetti and Leather, 2005). However, different views exist (Hoponainen and Peltonen, 2002; Wilkinson et al., 2002; Ougham et al., 2005; Schaefer and Rolshausen, 2006; Sinkkonen, 2006). Archetti (2000) specifically rejects the possibility that the bright autumn leaf coloration is aposematic. In the other studies favoring the signaling hypothesis (Hamilton and Brown, 2001; Hagen et al., 2003, 2004; Archetti and Brown, 2004; Archetti and Leather, 2005; Sinkkonen, 2006), aposematism is not discussed at all. The sixth system is a variety of color patterns enabling plants to mimic insects so as to reduce herbivory: mimicry of butterfly eggs (Benson et al., 1975; Shapiro, 1981; Williams and Gilbert, 1981), of ants, of aposematic caterpillars, and of aphids (Lev-Yadun and Inbar, 2002). The seventh system is aposematic coloration of spiny or poisonous plants, which has recently been proposed to reduce herbivory (Lev-Yadun, 2001, 2003a,b, 2006a; Midgley et al., 2001; Lev-Yadun and Ne'eman, 2004; Midgley, 2004; Rubino and McCarthy, 2004; Ruxton et al., 2004; Speed and Ruxton, 2005; Halpern et al., 2007). Ruxton et al. (2004) note that conspicuous aposematic thorns are a case of self-advertisement, as they manifest their own quality, unlike poisonous organisms that advertise their nasty character by an indirect coloration signal. Two related types of defensive plant coloration that might signal animals about their nutritive or defensive qualities are delayed greening of young leaves in the tropics (Kursar and Coley, 1992) and leaves that have different coloration on their adaxial and abaxial sides, or other kinds of color patterns in all types of ecosystems, which undermine herbivorous insect camouflage (Lev-Yadun et al., 2004; Lev-Yadun, 2006a).

Of the various colorful plant/animal communication systems, adaptive color changes are known to take part in the two extensively studied gene dispersal systems (pollination and frugivory). Young and unrewarding animal-pollinated flowers and young and unripe fleshy fruits are usually green and cryptic. Fleshy fruit usually become colorful only toward ripening, when they become edible by lowering the content of protective, poisonous, and otherwise harmful secondary metabolites, and by increasing their sugar, protein, fat content, flavor, and softness (Ridley, 1930; van der Pijl, 1982; Snow and Snow, 1988; Willson and Whelan, 1990).

Fruits usually change color from green when unripe to yellow, pink, orange, red, brown, blue, purple, or black when ripe (van der Pijl, 1982; Willson and Whelan, 1990), a phenomenon also considered to be at least partly adaptive (Willson and Whelan, 1990). Flowers usually become colorful and conspicuous only towards anthesis, when they open and offer nectar and pollen as rewards to pollinators. Many flowers retain their conspicuous advertising colors till they wilt. However, many others change their color after pollination (Weiss, 1991, 1995; Weiss and Lamont, 1997). Color change of flowers in an inflorescence may reduce its advertisement intensity, hence its detectability by pollinators. On the other hand, retaining the coloration after pollination, or after they turn unreceptive, may reduce pollinator visits to un-pollinated flowers, thus diminishing the plant's reproductive success. By the simultaneous reduction of reward after pollination and of attractiveness by changing their color, plants direct pollinators to un-pollinated flowers within the same inflorescence or plant. Floral color change is a well-documented phenomenon in various taxa and life forms on all continents (Weiss, 1991, 1995; Weiss and Lamont, 1997; Bradshaw and Schemske, 2003).

Here we describe and discuss the potential significance of color changes in senescent colorful aposematic prickles, spines, and thorns.

MATERIALS AND METHODS

As part of a broader study on defensive coloration in plants (Lev-Yadun, 2001, 2003a,b, 2006a,b; Lev-Yadun and Inbar, 2002; Lev-Yadun et al., 2002, 2004; Lev-Yadun and Ne'eman, 2004; Halpern et al., 2007), we observed plants whose prickles, spines, and thorns change color as they age. We focused on perennial plants, although annuals also show this character. This study was conducted to demonstrate the overlooked phenomenon of color change in thorns and spines, not to analyze that character in a whole flora or taxa.

RESULTS

The specific cases shown here (Table 1) were chosen to demonstrate this phenomenon in various taxa of several life forms, geographical distribution, and ecologies. The color change occurring along with the maturation of the protected organ makes the prickles, spines, and thorns less conspicuous. For instance, in species of *Rosa*, when the branches are young and green, the yellow, orange, red, brown, or black prickles are conspicuous. Later, when the branch changes its color from green to brown or gray, the prickles that have lost their original

Table 1
Differential discoloration in young vs. old prickles, thorns, and spines

Taxon	Color of mature prickles, spines, thorns, and background tissue	Color of old prickles, spines, thorns, and background tissue	Comments
Gymnosperms			
<i>Pinus taeda</i>	brown thorns on green	gray thorns on brown	in seed cones (T) [A]
<i>Pinus contorta</i>	brown thorns on green	gray thorns on brown or gray	in seed cones (T) [A]
<i>Araucaria araucana</i>	brown thorns on green	brown thorns on brown	in leaves (T) [A]
Angiosperms (monocotyledons)			
<i>Phoenix dactylifera</i>	yellow and black on green	brown on brown	leaflets (T) [AF, AS]
<i>Washingtonia filifera</i>	orange or brown on green	whitish spines on gray	along petioles (T) [A]
<i>Yucca aloifolia</i>	dark brown on green	gray on gray	end of leaves (T) [A]
Angiosperms (dicotyledons)			
<i>Calicotome villosa</i>	black on green	gray on gray	branch tips (S) [AS]
<i>Capparis spinosa</i>	yellow or orange on green or red	gray on gray	along branches (S) [AS, E]
<i>Carrisa grandiflora</i>	orange or red on green	gray on gray	along branches (S) [AF]
<i>Cereus peruvianus</i>	orange and brown on green	gray on gray	along stems (T) [A]
<i>Chorisia speciosa</i>	red on green	whitish or gray on green or gray + growth of new red prickles among the old ones	along trunk and branches (T) [A]
<i>Crataegus aronia</i>	red	gray	thorns (T) [AS]
<i>Erythrina corallodendrum</i>	black on green or gray	whitish on gray	along branches and trunk (T) [A]
<i>Euphorbia miltii</i>	reddish brown on gray	gray on gray	along trunk and branches (S) [AF]
<i>Rosa species</i>	yellow, orange, red, brown or black on green	whitish on brown	along stems (S) [A, AS, E]
<i>Rubus sanguineus</i>	yellow, orange or red on green or red	gray on gray	along stems (C) [AS]
<i>Ziziphus spina-christi</i>	orange-brown on gray	gray on gray	along branches (T) [AF, AS]
<i>Ziziphus lotus</i>	pink, red, brown on gray	gray on gray	along branches (S) [AF, AS]

(C) = climber; (S) = shrub; (T) = tree; [A] = America; [AF] = Africa; [AS] = Asia; [E] = Europe.

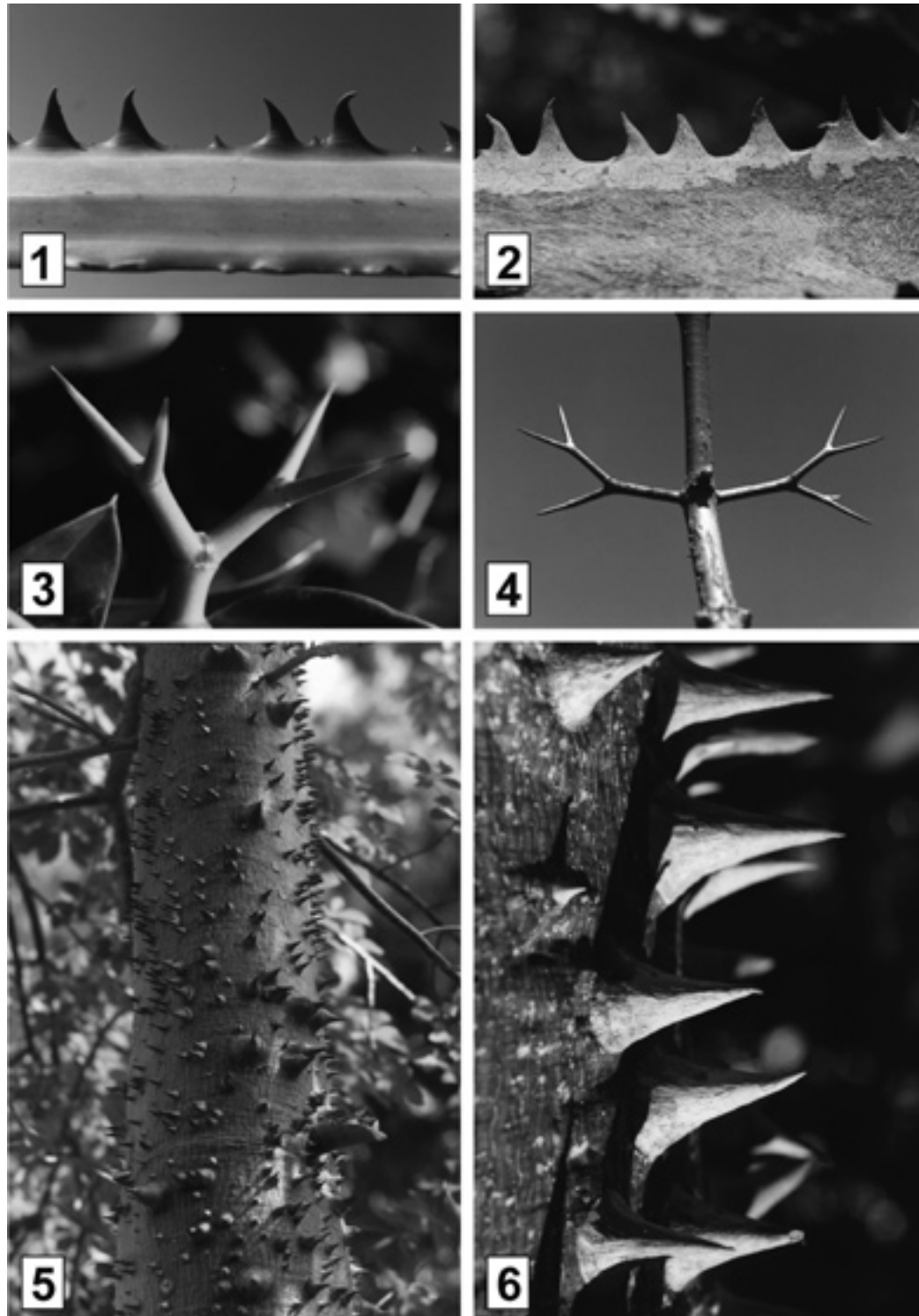


Fig. 1. Conspicuous brown spines along the petiole of the large, young, and green leaves of the American palm *Washingtonia filifera*. Fig. 2. Non-conspicuous gray spines along the dead, dry, and gray petiole of the large leaves of the American palm *Washingtonia filifera*. Fig. 3. Conspicuous thorns with red, sharp ends of live green branches *Carissa grandiflora*. Fig. 4. Non-conspicuous gray thorns of old, cork-covered branches *Carissa grandiflora*. Fig. 5. Conspicuous reddish prickles on the green young trunk of *Chorisia speciosa*. Fig. 6. Less-conspicuous whitish prickles on an older trunk of *Chorisia speciosa*.

coloration and have changed their color to white are much less conspicuous and aposematic. In other species [e.g., *Araucaria araucana* (Molina) K. Koch, *Washingtonia filifera* Wendl. (Figs. 1,2), *Carissa grandiflora* A. DC. (Figs. 3,4)], the color changes make them much less conspicuous and the spines and thorns lose all or most of their aposematic function (e.g., the spines along the margins of the petioles of the large leaves of the palm *Washingtonia filifera*, which have the same brown or gray color as the dry and dead petiole). *Chorisia speciosa* St.Hil., an American tree, has large red prickles (Fig. 5), several centimeters long, on its young green stems and branches. These original prickles change their color to whitish (Fig. 6) after several years. As the trees expand in girth, new red, conspicuous prickles form between the groups of old whitish prickles that have lost their color. The tree trunk, however, with its new groups of red prickles, remains conspicuous and aposematic.

DISCUSSION

While the adaptive significance and the broad occurrence of color change in flowers (Weiss, 1991, 1995), fruits (van der Pijl, 1982; Willson and Whelan, 1990), and leaves (Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004; Schaefer and Wilkinson, 2004; Lev-Yadun et al., 2004) has been discussed, the phenomenon of color change in spines, thorns, and prickles has never been described as a broad phenomenon and discussed as such. The scale of this phenomenon on a flora, on a continent, or globally is yet unknown. Here we describe for the first time this phenomenon and propose a function. We emphasize that color change in spines, thorns, and prickles is not mandatory, although it is common. We suggest that the color changes in senescent aposematic prickles, spines, and thorns are adaptive. The adaptive value may lie in reducing the investment in coloration, since the ephemeral thin coloration layer demands less resources. Keeping a prickle, spine, or thorn colorful for a long time is costly, and the benefit of being aposematic is smaller in older, larger, or otherwise better protected organs. However, theoretically a simple alternative explanation exists: the thorns, spines, and prickles are colorful simply because the hard polymers composing them are colorful by nature. We dismiss this possibility because the prickles, spines, and thorns that lose or change color remain hard and functional. The layer of coloration seems not to have a significant role in producing the sharpness of the prickles, spines, and thorns.

The cost to the plant of producing colored organs has three aspects. First, it requires allocation of resources for the synthesis of the pigments. Second, any color of

a plant's organ, other than green, is linked to lower photosynthesis and productivity. Third, conspicuousness may attract herbivores. We hypothesize that the color changes discussed here are adaptive, providing some advantage to the plant, and their expression depends on the reduced vulnerability of the defended organ to large herbivores correlated with its growth or maturity.

The tendency of plants to lower the cost of defense by prickles, spines, and thorns is a well-known phenomenon. For instance, African acacias and other woody plants have longer thorns on the lower branches than on the higher (White, 1988; Milewski et al., 1991; Brooks and Owen-Smith, 1994; Young and Okello, 1998; Gowda and Palo, 2003). Certain trees (e.g., various citrus) have large thorns only when juvenile and none when mature. Moreover, like several other types of induced defenses, spines and thorns are known to increase in size and number following herbivory (e.g., Milewski et al., 1991; Perevolotsky and Haimov, 1991; Young et al., 2003). We see no theoretical difficulty in proposing that color changes in prickles, spines, and thorns also reflect conservation of resources.

The broad taxonomic distribution of color changes in prickles, spines, and thorns indicates that this character has evolved repeatedly and independently in both Gymnosperms and Angiosperms, probably in response to selection by visually oriented herbivores.

REFERENCES

- Archetti, M. 2000. The origin of autumn colours by coevolution. *J. Theor. Biol.* 205: 625–630.
- Archetti, M., Brown, S.P. 2004. The coevolution theory of autumn colours. *Proc. R. Soc. London B* 271: 1219–1223.
- Archetti, M., Leather, S.R. 2005. A test of the coevolution theory of autumn colours: colour preference of *Rhopalosiphum padi* on *Prunus padus*. *Oikos* 110: 339–343.
- Benson, W.W., Brown, K.S., Gilbert, L.E. 1975. Coevolution of plants and herbivores: passion flower butterflies. *Evolution* 29: 659–680.
- Bradshaw, H.D.Jr., Schemske, D.W. 2003. Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* 426: 176–178.
- Brooks, R., Owen-Smith, N. 1994. Plant defences against mammalian herbivores: are juvenile *Acacia* more heavily defended than mature trees? *Bothalia* 24: 211–215.
- Clegg, M.T., Durbin, M.L. 2003. Tracing floral adaptations from ecology to molecules. *Nature Rev. Genet.* 4: 206–215.
- Cooper, S.M., Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68: 446–455.
- Darwin, C. 1877. *The different forms of flowers on plants of the same species.* John Murray, London.
- Facelli, J.M. 1993. Experimental evaluation of the foliar flag

- hypothesis using fruits of *Rhus glabra* (L.). *Oecologia* 93: 70–72.
- Faegri, K., Pijl, L. van der. 1979. The principles of pollination ecology. 3rd ed. Pergamon Press, Oxford.
- 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.
- Gowda, J.H. 1996. Spines of *Acacia tortilis*: what do they defend and how? *Oikos* 77: 279–284.
- Gowda, J.H., Palo, R.T. 2003. Age-related changes in defensive traits of *Acacia tortilis* Hayne. *Afr. J. Ecol.* 41: 218–223.
- 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.
- Hagen, S.B., Folstad, I., Jakobsen, S.W. 2003. Autumn colouration and herbivore resistance in mountain birch (*Betula pubescens*). *Ecol. Lett.* 6: 807–811.
- Hagen, S.B., Debeausse, S., Yoccoz, N.G., Folstad, I. 2004. Autumn coloration as a signal of tree condition. *Proc. R. Soc. London B* 271 (Suppl): S184–S185.
- Halpern, M., Raats, D., Lev-Yadun, S. 2007. Plant biological warfare: thorns inject pathogenic bacteria into herbivores. *Environ. Microbiol.* 9: 584–592.
- Hamilton, W.D., Brown, S.P. 2001. Autumn tree colours as a handicap signal. *Proc. R. Soc. London B* 268: 1489–1493.
- Holopainen, J.K., Peltonen, P. 2002. Bright autumn colours of deciduous trees attract aphids: nutrient retranslocation hypothesis. *Oikos* 99: 184–188.
- Janzen, D.H. 1986. Chihuahuan Desert nopaleras: defaunated big mammal vegetation. *Annu. Rev. Ecol. Syst.* 17: 595–636.
- Joel, D.M., Juniper, B.E., Dafni, A. 1985. Ultraviolet patterns in the traps of carnivorous plants. *New Phytol.* 101: 585–593.
- Kursar, T.A., Coley, P.D. 1992. Delayed greening in tropical leaves: an antiherbivore defense? *Biotropica* 24: 256–262.
- 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.* 244: 183–188.
- Lev-Yadun, S. 2003b. Why do some thorny plants resemble green zebras? *J. Theor. Biol.* 244: 483–489.
- Lev-Yadun, S. 2006a. 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. 2006b. Defensive functions of white coloration in coastal and dune plants. *Isr J. Plant Sci.* 54: 327–333, this issue.
- Lev-Yadun, S., Inbar, M. 2002. Defensive ant, aphid and caterpillar mimicry in plants. *Biol. J. Linn. Soc.* 77: 393–398.
- Lev-Yadun, S., Ne'eman, G. 2004. When may green plants be aposematic? *Biol. J. Linn. Soc.* 81: 413–416.
- Lev-Yadun, S., Dafni, A., Inbar, M., Izhaki, I., Ne'eman, G. 2002. Colour patterns in vegetative parts of plants deserve more research attention. *Trends Plant Sci.* 7: 59–60.
- Lev-Yadun, S., Dafni, A., Flaishman, M.A., Inbar, M., Izhaki, I., Katzir, G., Ne'eman, G. 2004. Plant coloration undermines herbivorous insect camouflage. *BioEssays* 26: 1126–1130.
- Midgley, J.J. 2004. Why are spines of African Acacia species white? *Afr. J. Range Forage Sci.* 21: 211–212.
- Midgley, J.J., Botha, M.A., Balfour, D. 2001. Patterns of thorn length, density, type and colour in African Acacias. *Afr. J. Range Forage Sci.* 18: 59–61.
- Milewski, A.V., Young, T.P., Madden, D. 1991. Thorns as induced defenses: experimental evidence. *Oecologia* 86: 70–75.
- Moran, J.A., Booth, W.E., Charles, J.K. 1999. Aspects of pitcher morphology and spectral characteristics of six Bornean *Nepenthes* pitcher plant species: implications for prey capture. *Ann. Bot.* 83: 521–528.
- Ougham, H.J., Morris, P., Thomas, H. 2005. The colors of autumn leaves as symptoms of cellular recycling and defenses against environmental stresses. *Curr. Topics Dev. Biol.* 66: 135–160.
- Perevolotsky, A., Haimov, Y. 1991. Structural response of Mediterranean woodland species to disturbance: evidence of different defense strategies. *Isr. J. Bot.* 40: 305–313.
- Ridley, H.N. 1930. The dispersal of plants throughout the world. L. Reeve & Co., Ashford, Great Britain.
- Rubino, D.L., McCarthy, B.C. 2004. Presence of aposematic (warning) coloration in vascular plants of southeastern Ohio. *J. Torr. Bot. Soc.* 131: 252–256.
- Ruxton, G.D., Sherratt, T.N., Speed, M.P. 2004. Avoiding attack. The evolutionary ecology of crypsis, warning signals & mimicry. Oxford University Press, Oxford.
- Schaefer, H.M., Rolshausen, G. 2006. Plants on red alert: do insects pay attention? *BioEssays* 28: 65–71.
- Schaefer, H.M., Wilkinson, D.M. 2004. Red leaves, insects and coevolution: a red herring? *Trends Ecol. Evol.* 19: 616–618.
- Shapiro, A.M. 1981. Egg-mimics of *Streptanthus* (Cruciferae) deter oviposition by *Pieris sisymbrii* (Lepidoptera: Pieridae). *Oecologia* 48: 142–143.
- Sinkkonen, A. 2006. Sexual reproduction advances autumn leaf colours in mountain birch (*Betula pubescens* ssp. *czerepanovii*). *J. Evol. Biol.* 19: 1722–1724.
- Snow, B., Snow, D. 1988. Birds and berries. A study of an ecological interaction. T. & A.D. Poyser, Calton, UK.
- Speed, M.P., Ruxton, G.D. 2005. Warning displays in spiny animals: one (more) evolutionary route to aposematism. *Evolution* 59: 2499–2508.
- Stiles, E.W. 1982. Fruit flags: two hypotheses. *Am. Nat.* 120: 500–509.
- Tomlinson, P.B. 1990. The structural biology of palms. Clarendon Press, Oxford.
- van der Pijl, L. 1982. Principles of dispersal in higher plants. 3rd ed. Springer-Verlag, Berlin.
- Weiss, M.R. 1991. Floral colour changes as cues for pollinators. *Nature* 354: 227–229.

- Weiss, M.R. 1995. Floral colour change: a widespread functional convergence. *Am. J. Bot.* 82: 167–195.
- Weiss, M.R., Lamont, B.B. 1997. Floral colour change and insect pollination: a dynamic relationship. *Isr. J. Plant Sci.* 45: 185–199.
- White, P.S. 1988. Prickle distribution in *Aralia spinosa* (Araliaceae). *Am. J. Bot.* 75: 282–285.
- Wilkinson, D.M., Sherratt, T.N., Phillip, D.M., Wratten, S.D., Dixon, A.F.G., Young, A.J. 2002. The adaptive significance of autumn leaf colours. *Oikos* 99: 402–407.
- Williams, K.S., Gilbert, L.E. 1981. Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. *Science* 212: 467–469.
- Willson, M.F., Hoppes, W.G. 1986. Foliar 'flags' for avian frugivores: signal or serendipity? In: Estrada, A., Fleming, T.H., eds. *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht, pp. 55–69.
- Willson, M.F., Whelan, C.J. 1990. The evolution of fruit color in fleshy-fruited plants. *Am. Nat.* 136: 790–809.
- Young, T.P., Okello, B.D. 1998. Relaxation of an induced defense after exclusion of herbivores: spines on *Acacia drepanolobium*. *Oecologia* 115: 508–513.
- 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. 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 Publishers, The Hague, pp. 287–295.