Arthropod-Plant Interactions (2013) 7:1–20
DOI 10.1007/s11829-012-9239-7

REVIEW ARTICLE

The role of carotenoids and their derivatives in mediating interactions between insects and their environment

Jeremy J. Heath · Don F. Cipollini ·
John O. Stireman III

Received: 16 March 2012 / Accepted: 28 November 2012 / Published online: 28 December 2012

Abstract Carotenoids are long conjugated isoprenoid molecules derived mainly from plants and microbial organisms. They are highly diverse, with over 700 identified structures, and are widespread in nature. In addition to their fundamental roles as light-harvesting molecules in photosynthesis, carotenoids serve a variety of functions including visual and colouring pigments, antioxidants and hormone precursors. Although the functions of carotenoids are relatively well studied in plants and vertebrates, studies are severely lacking in insect systems. There is a particular dearth of knowledge on how carotenoids move among trophic levels, influence insect multitrophic interactions and affect evolutionary outcomes. This review explores the known and potential roles that carotenoids and their derivatives have in mediating the ecological interaction of insects with their environment. Throughout the review, we highlight how the fundamental roles of carotenoids in insect physiology might be linked to ecological and evolutionary processes.

Keywords Apocarotenoids · Chemical ecology · Plant hormones · Abscisic acid · Strigolactones · Insect semiochemicals

Introduction

Carotenoids are life-sustaining molecules. They play such a critical role in photosynthesis that all life in an oxygenated environment depends on them (Britton 1995a). Carotenoids are one of the most ubiquitous groups of organic molecules known, but how they function in modulating insect–environment interactions is only beginning to be understood. In general, they are long conjugated chains of carbon with rings on either end, which may contain oxygenated functional groups. Carotenoids are essential in photosynthesis to harvest light energy and protect chlorophyll in times of excess light energy by quenching reactive oxygen species that are produced during photosynthesis and plant stress. In animals, their bright yellow to red colour is employed as mating signals and aposematic colouration. Although it is just beginning to be investigated, there is growing evidence that carotenoids are important mediators of ecological interactions in insects. Further research into the roles of carotenoids and their derivatives in insect ecology promises to dramatically expand our comprehension of their varied functions and importance (Blount and McGraw 2008).

Although Czeczuga et al. have published extensively on the quality and quantity of carotenoids in a number of organisms, including nearly all major groups of arthropods (Czeczuga 1976, 1980; Czeczuga and Mironiuk 1980; Czeczuga 1981, 1982; Czeczuga and Weyda 1982; Czeczuga 1985, 1986, 1988, 1990, 1991), and some functions of carotenoids in insects have been examined elsewhere (Fox 1976; Goodwin 1986; Blount and McGraw 2008), no broad review of the ecological roles of carotenoids in insects exists. Here, we explore the natural functions of carotenoids in insects with a focus on the known and potential modulating roles that carotenoids or their derivatives play in insect multitrophic and environmental interactions. These modulating functions may contribute significantly to shaping the evolution of many insect taxa.

We begin with a brief overview of carotenoid structures, nomenclature and biosynthesis. We then briefly review the

Handling Editor: Gary Felton.

J. J. Heath (✉) · D. F. Cipollini · J. O. Stireman III
Department of Biological Sciences, Environmental Sciences
PhD Program, Wright State University, 3640 Colonel
Glenn Hwy, Dayton, OH 45435, USA
e-mail: heath.22@wright.edu

diversity and functions of carotenoids in plants and discuss their uptake by insects. We review some of the key functions of carotenoids in insects, illustrating their fundamental importance with particular focus on the varied roles of carotenoids in mediating insect–plant interactions. Finally, we consider the roles of carotenoids in mediating multitrophic interactions. Throughout the review, we highlight areas in need of more research and attempt to link the fundamental physiological (or internal) roles of carotenoids with their more ecological (or external) functions. The varied and essential functions of carotenoids in insects as well as their diet-dependent uptake may provide a series of model systems well suited to studying niche specialization and the complex and poorly understood relationship between phenotype and genotype (Badyaev 2011 and references therein).

Nomenclature and structures

There are over 700 different identified carotenoid molecules and many more if all the potential isomers are considered; for instance, there are theoretically 1,056 possible (E/Z)-isomers of lycopene and 272 for β,β-carotene (Pfander 1992). Furthermore, carotenoids often have chiral centres, which greatly increase the number of possible isomers. However, naturally occurring carotenoids are generally in the all-E form and certain chiral structures predominate.

Carotenoids are divided into two groups: carotenes and xanthophylls. The carotenes are hydrocarbons and the xanthophylls are their oxygenated derivatives. Carotenoids derive much of their diversity from the addition of a number of different functional groups, which are most commonly attached to the rings or the ends of the molecule, but rarely to the centre. Most of the tetraterpenoids (i.e. carotenoids with 40 carbon atoms) are named by adding prefixes to the name 'carotene'. These prefixes are Greek letters corresponding to the end groups. Note that both end groups are written to be unambiguous. For example, the carotenoid generally known as β-carotene is unambiguously named as β,β-carotene (Fig. 1). Those carotenoids with fewer than 40 carbon atoms are called apocarotenoids if the loss of atoms occurs at one end of the molecule, diapocarotenoids if it occurs at both ends and norcarotenoids if it occurs within the molecule. These shortened structures are also generally referred to as norisoprenoids (Britton 2008).

Carotenoids are orange because of the large light-absorbing chromophore in the centre of the molecule. This sequence of conjugated double bonds absorbs light at about 450 nm and dissipates the energy as heat. Higher wavelengths of light are reflected, giving them their characteristic orange colour. The extended chromophore of lycopene absorbs more of the yellow–orange light and thus reflects red light. Carotenoids vary in their absorption maxima, which is useful for identification.

Carotenoid biosynthesis and diversity in plants

In plants, carotenoids are synthesized from precursors derived from the methylerythritol-4-phosphate (MEP) pathway in plastids (reviewed by Eisenreich et al. 2001, Hirschberg 2001). Generally, 3 units of isopentenyl diphosphate (IPP) and one unit of dimethyl allyl diphosphate (DMAPP) from the MEP pathway condense to form geranylgeranyl diphosphate (GGPP, C20) in plastids; two units of GGPP condense to form phytoene (Dudareva et al. 2006). Four rounds of phytoene dehydrogenation lead to lycopene, which can undergo cyclizations, dehydrogenations and oxidations to form numerous carotenoid molecules. In plants and algae, monoterpenes, diterpenes and carotenoids are synthesized similarly in the plastids (Lichtenthaler 1999). Movement of precursors from the plastids (MEP pathway) to the cytosol (mevalonic acid pathway) also occurs (Bartram et al. 2006; Dudareva et al.

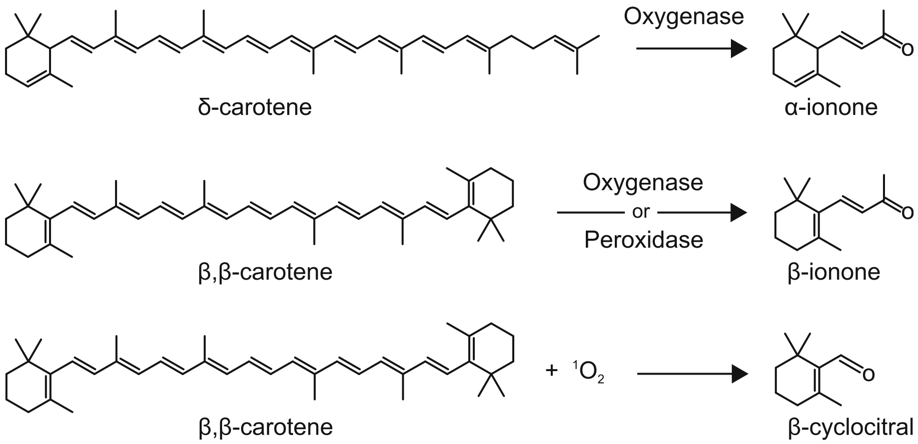

Fig. 1 Three examples of carotenoids degrading to volatile apocarotenoids (α-, β-ionone and β-cyclocitral) via carotenoid cleavage oxygenases (Ibdah et al. 2006), fungal peroxidases (Zorn et al. 2003) or singlet oxygen (Ramel et al. 2012)

2006) and may contribute to the formation of sesquiterpenes, sterols (triterpenes) and polyterpenes in the cytosol (Lichtenthaler 1999). Functional groups may be added in the cytosol as well (Grunewald et al. 2001).

The diversity of carotenoids in plant leaves (i.e. chloroplasts) is generally low with components of the xanthophyll cycle (i.e. **violaxanthin**, antheraxanthin and zeaxanthin), **β,β-carotene**, **lutein**, **neoxanthin**, β,ε-carotene, β-cryptoxanthin and lutein 5,6-epoxide being the most commonly occurring. The carotenoids in bold above are generally found at the highest concentrations in leaves and lactucaxanthin occurs in some species such as lettuce (Britton 1995b; Britton et al. 2004). Lycopene is a precursor to all of these, but the metabolic pull is likely so strong that it does not accumulate in the leaves. However, lycopene is a common component of red fruits such as tomato and pepper where photosynthesis is low or non-existent. Carotenoids often contribute to flower colour, but interestingly the majority of flower pigments are phenolics (i.e. anthocyanins). Fruit and flower carotenoids are often xanthophylls and as such they can be and often are conjugated to fatty acids (Britton 1995b), which require saponification to release the free carotenoid for proper identification. This is frequently the case for insect xanthophylls as well.

Carotenoid derivatives

Flavour chemists have long been aware of the production of volatile chemicals from the degradation of carotenoids (Stevens 1970). Numerous in vitro studies have shown that oxygenase, peroxidase and possibly lipoxygenase (Walter and Strack 2011) enzymes from microbes and plants have the capacity to cleave carotenoids to form volatile apocarotenoids (Zorn et al. 2003; Simkin et al. 2004; Baldermann et al. 2005; Bouvier et al. 2005; Lewinsohn et al. 2005a; Lewinsohn et al. 2005b; Auldridge et al. 2006; Goff and Klee 2006; Ibdah et al. 2006; Garcia-Limones et al. 2008; Scherzinger and Al-Babili 2008; Vogel et al. 2008). In addition, singlet oxygen is capable of cleaving carotenoids on its own and the products can have hormonal properties (Ramel et al. 2012).

Lewinsohn et al. (2005b) showed that a mutant tomato plant and a watermelon cultivar, both extremely deficient in lycopene, produced much less geranial and neral (which are insect semiochemicals, Table 1) compared to high lycopene producers, suggesting that these volatiles were produced via lycopene degradation. This could be explained by a general decrease in the terpenoid pathway, since these compounds are both monoterpenes (C_{10}). However, the reason the mutant tomato did not produce lycopene was because it had a defective phytoene synthase, which would leave the upstream portion of terpenoid synthesis intact. As another example, β-ionone is easily generated via cleavage of β,β-carotene by the oxygenase CmCCD1 (Fig. 1) and white flesh melon plants deficient in β,β-carotene substrate, but with expression of CmCCD1, lack the production of β-ionone (Ibdah et al. 2006). Additionally, the same oxygenase can generate α-ionone from the cleavage of a δ-carotene (Fig. 1), geranylacetone from phytoene and pseudoionone from lycopene (Ibdah et al. 2006). Singlet oxygen reacts with β,β-carotene to form a range of hormonally active apocarotenoids (Fig. 1; Ramel et al. 2012). Studies similar to these are numerous and have illustrated the production of a variety of apocarotenoids, which may be very important as insect semiochemicals (Table 1).

Carotenoid acquisition by insects

Although animals can modify carotenoids (e.g. cleave and add functional groups), they generally cannot synthesize them *de novo* (Kayser 1982; Walter and Strack 2011). One study reported β,β-carotene being synthesized by cockroaches (Shukolyukov and Saakov 2001); however, the authors acknowledged that the potential contribution of symbiotic microorganisms could not be ruled out. In two recent studies (Moran and Jarvik 2010; Altincicek et al. 2011), genes laterally transferred from a fungus and integrated into arthropod genomes (i.e. aphids and mites) appear responsible for the *de novo* biosynthesis of torulene and related carotenoids, but how widespread these genes might be in insects is not known.

Insects generally sequester carotenoids in proportion to the concentration found in the diet (Feltwell and Rothschild 1974; Ahmad and Pardini 1990) and this often results in accumulation of lutein, which is the most dominant carotenoid in angiosperms (Pogson et al. 1996). However, they can also concentrate specific carotenoids in specific tissues with the aid of carotenoid binding proteins and active transport mechanisms (Kiefer et al. 2002; Bhosale and Bernstein 2007; Sakudoh et al. 2007) and this can be under hormonal control (Starnecker 1997). Mobile insects may also selectively feed on plants or plant parts to bolster their carotenoid intake in response to environmental stress or enemy attack (Smilanich et al. 2011). Stereospecific oxidative transformation of dietary carotenoids is common in insects resulting in a diversity of final carotenoid molecules in insect tissues, but these usually have structural backbones that represent their dietary source (Kayser 1982).

Diversity of carotenoid functions in insects

Carotenoids play many important roles in insect structure, physiology and life history. They provide colouration; are

Table 1 Some apocarotenoids known to be generated by oxidative cleavage of carotenoids and have biological activity in plants, animals or microorganisms

Name	Functions	Pherobase citations[a]	References[b]
Retinal, retinoic acid, retinol	Vision, morphogen	None	1
Abscisic acid	Plant hormone	None	1
Strigolactones	Plant hormone, fungal growth	None	1,2,3
Mycorradicin	Antifungal properties	None	1
Blumenin	Antifungal properties	None	1
Trisporic acid	Fungal pheromone	None	1
β-Cyclocitral	Fruit flavour, floral volatile	F^{12}	1,13,16
4-Oxoisophorone	Fruit flavour, floral volatile	F^{180}	11,13
Pseudoionone	Fruit flavour, floral volatile	F^{155}	12,13
(E)-β-damascenone	Fruit flavour, floral volatile	F^{158}	6,13
β-ionone, α-ionone, 3-hydroxy-β-ionone, 3-hydroxy-α-ionone, 3-hydroxy-5,6-epoxy-β-ionone	Fruit flavours, floral volatiles, insect semiochemicals	F^{355,203,0,0,0}Ha^{7,0,0,0,0} Ca^{2,1,0,0,0}Da^{1,1,0,0,0} Dk^{1,0,0,0,0}	1,4, 5,13,16
Geranylacetone	Fruit flavour, floral volatile, insect semiochemicals	F^{396}Hp^{10}Ha^{2}Hk^{1}Hal^{1}Da^{1}Mk^{1}HETa^{1}	12,13
(E)-3,7-Dimethyl-2,6-octadienal Aka: geranial or citral a	Floral volatile, insect semiochemicals	F^{384}Hp^{24}Sp^{18}Cal^{5}Bp^{3}HETp^{1}Ha^{1}THYp^{1}	13,15
(Z)-3,7-Dimethyl-2,6-octadienal Aka: neral or citral b	Floral volatile, insect semiochemicals	F^{330}Cal^{4}Hp^{4}Ha^{1}Bp^{2} Sp^{2}DIal^{1}Ca^{1}Dal^{1}Da^{1}	13,15
Sulcatone, sulcatol	Floral volatiles, insect semiochemicals	F^{490,205}Hp^{21,3}Da^{6,0} Cal^{5,0}Hal^{4,0}Cp^{1,3}Ha^{2,1}Ca^{1,2}Mp^{1,1}Tp^{1,1} HETa^{1,1}HETp^{1,0}Hk^{1,0}Bal^{1,0}Bp^{1,0}Ba^{1,0}Sk^{1,0}	8,9, 10,13
Edulan II[c] Dihydroedulan I 9,10-Epoxytetrahydroedulan[c] 1,5,5,9-Tetramethyl-10-oxabicyclo[4.4.0]-3-decen-2-one[c] 2,2,6,8-Tetramethyl-7-oxabicyclo[4.4.0]-4-decen-3-one[c]	Floral volatile, insect semiochemical	F^{154,4,0,0,0} Bp^{0,1,1,1,1}	7,13
Dihydroactinidiolide	Floral volatile, insect semiochemical	F^{157}Bp^{2}	7,13, 14,16

[a] Pherobase (El-Sayed 2011) citations are represented by a letter code with superscripts. The first set of uppercase letters indicates the Arthropod group except for **f**loral volatiles (F): **Het**eroptera (HET), **H**ymenoptera (H), **C**oleopteran (C), **D**iptera (D), **M**oths (M), **B**utterflies (B), **T**richoptera (T), **S**piders and mites (S), **Di**ctyoptera (DI), **Thy**sanoptera (THY). The lowercase letters that follow the group code stand for behavioural significance: **p**heromone component (p), **a**ttractant (a), **k**airomone (k) or **al**lomone (al). The superscript order is with respect to the order in the 'name' column and indicates the number of species that release the component listed in Pherobase

[b] References: (1) Auldridge et al. 2006; (2) Pichersky 2008; (3) Umehara et al. 2008; (4) Williams et al. 2000; (5) Garcia-Limones et al. 2008; (6) Ferreira et al. 2008; (7) Schulz et al. 1993; (8) Aplin and Birch 1970; (9) Birch 1970; (10) Gao et al. 2008; (11) Goff and Klee 2006; (12) Ibdah et al. 2006; (13) El-Sayed 2011; (14) Dudareva et al. 2006; (15) Lewinsohn et al. 2005a, Lewinsohn et al. 2005b, (16) Ramel et al. 2012

[c] These compounds are not known to be generated from carotenoid cleavage, but their structures are suggestive

involved in vision, diapause and photoperiodism; serve as antioxidants; mating signals and precursors to pheromones. In order to understand their importance in ecological interactions, we first review some of their known functions in insects and then concentrate on their specific roles in mediating multitrophic interactions.

Colouration

Many insects use carotenoids to colour various portions of their bodies, eggs or even galls (Feltwell and Rothschild 1974; Davidson et al. 1991; Inbar et al. 2010a; Inbar et al. 2010b; White 2010), but few studies have investigated their adaptive significance (Oberhauser et al. 1996). The abundance of brightly coloured, sexually dimorphic butterflies would suggest that carotenoids are important in mate choice, but no studies have shown that carotenoids are involved in butterfly wing colour (Nijhout 1991; Shawkey et al. 2009). In monarchs, male wing colour does influence mating success, but the source of the orange wing colouration has not been identified (Davis et al. 2007).

Vision, diapause and photoperiodism

As in vertebrate systems, carotenoids are important to invertebrates as precursors to visual pigment chromophores such as retinal or 3-hydroxyretinal. The involvement of carotenoids in insect vision has been known for decades, but a recent key connection was made by Von Lintig et al. (2001) who found that blindness in a mutant *Drosophilia* strain is due to a dysfunctional carotenoid cleavage dioxygenase that is responsible for biosynthesizing Vitamin A, the direct precursor to the visual chromophores. Many other invertebrates have also been shown to require carotenoids or diet-derived Vitamin A to biosynthesize visual pigment chromophores (Stavenga 2006). The clear physiological and likely pleiotropic genetic connection between sequestration of carotenoids for vision and the induction of carotenoid-based colour polyphenisms in some lepidopteran larvae warrants further investigation.

While the mechanism of photoperiodic induction of diapause in arthropods has not been fully elucidated, carotenoids are clearly involved. The photoperiod induction of diapause requires carotenoids (or Vitamin A) in spider mites, moths, wasps and butterflies (Veerman 2001). The photoreceptor associated with photoperiod measurement appears to be an opsin receptor that requires Vitamin A (Veerman and Veenendaal 2003), while entrainment of the circadian rhythm is independent of vitamin A or carotenoids (Veerman 2001). It is not hard to imagine how the fundamental requirement for carotenoids in vision and diapause may dramatically influence ecological and evolutionary outcomes (Fig. 2), but to our knowledge, no studies have made this potential connection.

Antioxidants

Several studies have demonstrated that carotenoids can act as antioxidants in insects. In mammals, ultraviolet (UV) radiation can enhance oxidative stress (Jurkiewicz and Buettner 1994; Shindo et al. 1994) and both UV radiation and oxidative stress are known to be damaging to arthropods (Ahmad and Pardini 1990; Aarseth and Schram 2002; Suzuki et al. 2009). Through a combination of blocking UV light, which activates prooxidant allelochemicals, and by direct quenching of singlet oxygen generated from prooxidant allelochemicals, carotenoids can protect vital cellular components from damage (Ahmad 1992; Carroll et al. 1997; Carroll and Berenbaum 2006). The abundance and diversity of carotenoids in particular insects may relate to the UV environment in which the species has evolved. Carotenoids can also contribute to the immune response in arthropods, probably by scavenging reactive oxygen species associated with up-regulation of the immune system (Ojala et al. 2005; Babin et al. 2010; Smilanich et al. 2011).

Mate choice and signalling

Volatile apocarotenoids are found as components of short-range courtship pheromones released from structures in male butterflies called hair-pencils and as pheromone components of many hymenopterans (Table 1). Males of *Pieris napi* butterflies produce citral, which is a mixture of the apocarotenoids neral and geranial (Fig. 2; Table 1). Odourless male models are always rejected by females, but both citral-laced models and freshly killed males stimulate female mate-acceptance behaviour (Andersson et al. 2007). In butterflies, these volatiles may be produced within the body from sequestered carotenoid precursors, although this has not been documented.

Roles of carotenoids and their derivatives in mediating insect–plant interactions

Mediation of oxidative stress

The antioxidant functions of carotenoids are likely a key feature in modulating insect–plant interactions as many plants produce photosensitized prooxidant compounds such as acetophenones, carboline alkaloids, furanochromes, furanocoumarins, furanoquinoline alkaloids, extended quinones, isoflavonoid phytoalexins, isoquinoline alkaloids, lignans, polyacetylenes and thiophenes (Berenbaum 1987). Metabolically activated compounds such as quinones and flavonoids are also important prooxidant allelochemicals. These compounds can react with molecular oxygen to produce a range of reactive oxygen species (ROS), including superoxide anion radical ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($^{\cdot}OH$), lipid hydroperoxides, peroxyl radicals and singlet oxygen ($^1O_2$). Of these, $^{\cdot}OH$ and $^1O_2$ are the most reactive and therefore damaging to cellular components such as membranes (Ahmad and Pardini 1990). Carotenoids are most effective against $^1O_2$ either through physical or chemical quenching (Fig. 1), the latter of which cleaves the carotenoid molecule into smaller volatile apocarotenoids (Stratton et al. 1993; Sommerburg et al. 2003; Ramel et al. 2012), but they can also scavenge peroxyl radicals (Sommerburg et al. 2003). Carotenoids can

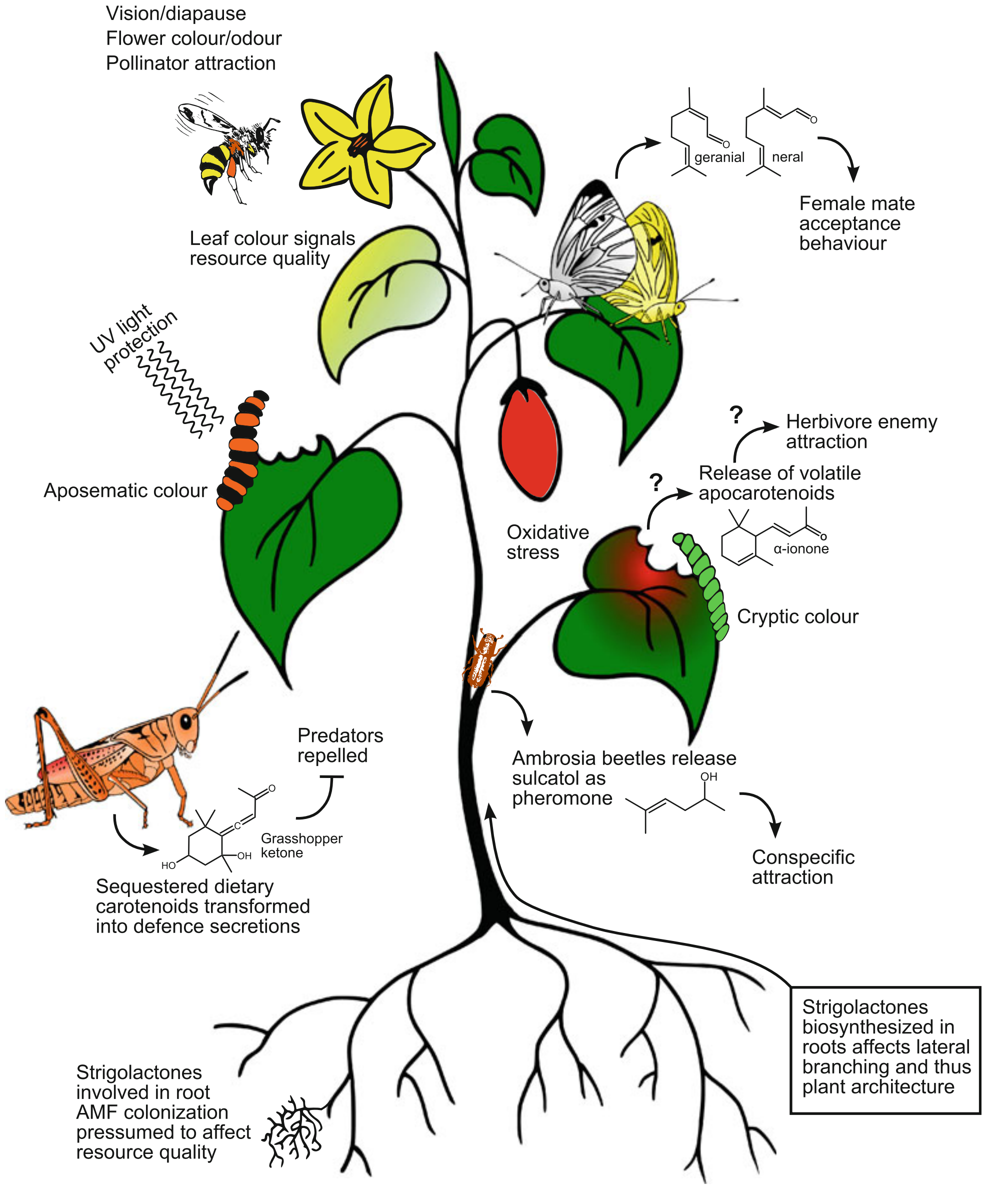

Fig. 2 A stylized, schematic representation of the various known and hypothesized functions of carotenoids in insects that mediate ecological interactions. See online colour version

also have significant indirect effects through the protection of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT), which work together to deactivate $O_2^{\cdot-}$. SOD converts $O_2^{\cdot-}$ to H_2O_2, which is rapidly converted to H_2O and O_2 by CAT before H_2O_2 forms the more damaging $^{\cdot}OH$ radical. Singlet oxygen and peroxyl radicals are known to inhibit SOD and CAT activity (Escobar et al. 1996) and thus carotenoids may play key roles in protecting insects and other organisms from both exogenous (e.g. via plant allelochemicals) and endogenous (e.g. via metabolic by-products) sources of ROS (Ahmad 1992).

Carroll et al. (1997) showed that parsnip webworms avoid damaging UVA light when reared on a carotenoid-free diet, but when the diet was amended with lutein (a xanthophyll) or the caterpillars were allowed to feed on their host plant, they did not avoid UVA radiation. UVA avoidance is of particular importance in this system because host plants contain UV-activated phototoxic furanocoumarins. Subsequently, Carroll and Berenbaum (2006) found a significant correlation between larval lutein concentration (i.e. sequestration) and daily UV irradiance in wild populations of webworms collected across an altitudinal/latitudinal UV gradient. More direct studies have also shown the benefits to insects of sequestered carotenoids. For example, β-carotene-amended diets provide significant protection from topical applications of alpha-terthienyl, a phototoxic phytochemical, in *Manduca sexta* larvae (Aucoin et al. 1990; Aucoin et al. 1995). And, an association between sequestration of carotenes and larval success has recently been documented in which carotene-sequestering larvae were much more likely to survive feeding on a toxic host plant (Shao et al. 2011).

The antioxidant properties of carotenoids may also augment the immune response in insects and other arthropods by scavenging ROS generated during this process (Cornet et al. 2007), but this may come with ecological costs associated with conspicuous pigmentation. Van der Veen (2005) showed a plastic regulation of carotenoid content in individual copepods in response to predation risk. Copepods that down-regulated their carotenoid content in response to elevated risk of predation were also more susceptible to parasite infection, suggesting a trade-off between predation avoidance and immunocompetence.

The antioxidant function of carotenoids in arthropods is an area in need of more study, particularly with respect to their roles in influencing interactions between herbivores and their host plants (Ahmad 1992; Felton and Summers 1995). The antioxidant properties of carotenoids may be enhanced by the presence of other antioxidants such as ascorbic acid or tocopherols (Catoni et al. 2008), but studies in arthropods are lacking. The importance of carotenoids in aposematism might be augmented by this potential positive interaction, since other potent antioxidants are colourless. The use of carotenoids as protective antioxidants may be important in shaping insect niches. They may allow herbivores to expand their dietary range to phototoxin-protected plants (or to specialize on such plants for their own defence), persist under conditions with high parasite pressure (Smilanich et al. 2011) or feed in more UV-rich habitats.

Carotenoids may also be important in managing oxidative stress associated with herbivory and pathogen attack in plants. Plants are predicted to benefit from limiting the spread of oxidative stress to localized tissues in order to limit the use of valuable antioxidants and to attract herbivore enemies. The cells closer to the damaged site are more likely to be in an oxidizing state and thus more conducive to the formation of apocarotenoids (Oliveira et al. 2011 and references therein). Attack by phytophagous insects and pathogens is known to cause the induction of several defensive pathways in plants (Maleck and Dietrich 1999). Bi and Felton (1995) showed unequivocally that the oxidative status of soybean plants changes after herbivory and that herbivores are negatively affected by this onslaught of oxygen radicals. Earlier work showed that pathogen infection resulted in a similar reaction (Mehdy 1994). During herbivory, antioxidants such as ascorbic acid, total carotenoids, non-protein thiols and catalase decreased systemically in plants (Bi and Felton 1995). The breakdown of carotenoids, chlorophylls and the production of VOCs may be symptomatic of autotoxicity or the result of strategic management of ROS by plants. Alternatively, these decreases may represent a strategy employed by herbivores and pathogens to overwhelm plant defences. One would predict that the intensity of this effect should increase with proximity to the damage site, thus explaining the more prevalent decrease in carotenoids and chlorophylls locally as opposed to systemically (see citations in the 'Tritrophic signalling' section below).

Resource signalling: colour

The essential physiological roles that carotenoids play in photosynthesis (Britton 1995a; Telfer et al. 2008) such as harvesting light energy and preventing photo-oxidative damage via the xanthophyll cycle (Demmig-Adams and Adams 1996) suggest that changes in host-plant carotenoid content should provide information to foraging herbivorous insects about the quality of the tissue, because photosynthesis ultimately provides carbon sources and energy for nitrogen fixation and/or assimilation. Conversely, if carotenoids correlate strongly with defensive chemicals, insects may be repelled.

W. D. Hamilton proposed that temperate deciduous plants signal their defences to herbivores via brightly coloured fall foliage (Archetti 2000). This idea is consistent with the finding that aphid diversity is greater on host plants with coloured fall foliage, suggesting a co-evolutionary history (Hamilton and Brown 2001). However, it may be more likely that coloured fall foliage is simply used as a cue rather than evolving as a signal (Schaefer and Rolshausen 2006). This controversial idea (Wilkinson et al. 2002) spurred a series of papers (reviewed in Lev-Yadun and Gould 2007) that proposed alternative ecological explanations for brightly coloured fall foliage. All of these hypotheses recognize the fact that the proximate reason for fall colour is to protect the plant from photoinhibition during chlorophyll scavenging and nitrogen storage when temperatures drop but light is still relatively intense. Theoretically, carotenoids could signal honestly to herbivores that the carotenoid biosynthetic pathway, which also leads to the biosynthesis of mono- and diterpenoids (Lichtenthaler 1999), is well established or still functioning. Monoterpenoids (De Moraes et al. 1998) and possibly apocarotenoids (see section 'Resource signalling: odour') are important attractants for natural enemies, while diterpenoids have demonstrated anti-herbivore properties (Gebbinck et al. 2002). Alternatively, it has been argued that green autumn leaves rather than coloured foliage should be more attractive to natural enemies and less nutritious to phloem-feeding aphids (Holopainen 2008). Although many studies have confirmed the physiological link between carotenoid quality/quantity and photosynthetic capacity (Telfer et al. 2008), only one study has shown that these pigment differences directly affect the behaviour and fitness of insect herbivores. Zheng et al. (2010) used gene-silencing techniques to show that plant tissues that lacked carotenoids and became photo-bleached were both less attractive to an ovipositing butterfly and less nutritious for its offspring than tissue from fully competent plants. Future studies in this regard will benefit from focusing on the fitness consequences of intraspecific host-plant variation in carotenoids where stabilizing or directional selection will likely be most obvious and quantifiable. Manipulative experiments designed to disrupt the biosynthesis of specific carotenoid pigment molecules would also be informative.

Many fruits and flowers derive their bright colours from carotenoids. In some cases, these colours may warn potential herbivores (particularly mammals) that the fruit is toxic, such as the red colour of capsaicin-containing red peppers; but more often these colours serve to attract seed dispersers and pollinators (Tewksbury and Nabhan 2001). Almost every orange or yellow fruit and many red fruits contain carotenoids. Indeed, the red colour of tomatoes is due mainly to the accumulation of the carotenoid lycopene.

The control of flower colour by carotenoid content is evident from breeding experiments and transgenic plants. Suzuki et al. (2007) were able to add a gene to the carotenoid biosynthetic pathway of *Lotus japonicus*, thus changing its flower colour from a lemon yellow to a bright orange. Ohmiya et al. (2006) changed wild-type white chrysanthemum flowers to yellow via RNA interference of a carotenoid cleavage dioxygenase (CCD) enzyme. These enzymes are widespread in plants and are very important in conferring odour and flavours to fruits and flowers. CCDs cleave carotenoid molecules at double bonds producing molecules with shorter chromophores that do not absorb visible light (see section 'Resource signalling: odour'). The colour of fruits and flowers can have dramatic ecological consequences (Whitney and Glover 2007); for instance, Bradshaw and Schemske (2003) illustrated an immense reversal in pollinator preference when they bred colour changes into the monkeyflowers *Mimulus lewisii* and *M. cardinalis*. Furthermore, mutant *M. lewisii* with reduced carotenoid-based nectar guides receive fewer successful bumblebee visits (Owen and Bradshaw 2011), but Dyer et al. (2007) warn of the possible confounding effects of not using completely isogenic lines. Regardless of whether isogenic lines are used, the potential for confounding effects seems likely because CCDs can change both colour and odour simultaneously.

The most obvious selective force maintaining fruit colour would seem to be seed-dispersing frugivores such as birds, but evidence for this is surprisingly scarce (Whitney and Stanton 2004). Whitney and Stanton (2004) have shown that pleiotropic effects (or possibly linkage) appear to maintain a carotenoid-derived fruit polymorphism in *Acacia ligulata* via selection by a heteropteran seed predator. Interestingly, carotenoids may also be important in mate signalling in this system because females develop a yellow colour on the legs at sexual maturity. A number of plants incorporate toxic secondary metabolites in their ripe fleshy fruits, an apparent contradiction to the dispersal hypothesis (Cipollini 2000). There seems to be a delicate balance between dispersal, predation and microbial degradation that must be optimized by plants over space and time (Cipollini 2000; Tewksbury et al. 2008).

Resource signalling: odour

Carotenoids may also play important roles as olfactory cues for insects and as olfactory signals by plants. Volatile apocarotenoids (i.e. derivatives of carotenoids) have a range of functions that can benefit the plant directly, indirectly or are detrimental. Many apocarotenoids are likely to be pollinator attractants, since they are highly represented in flower volatiles (Table 1), including those of orchids (El-Sayed 2011). Interestingly, many also appear to be hymenopteran pheromones (Table 1) and some act as courtship pheromones in butterflies. Apocarotenoids are also associated with the flavour and odours of ripe fruit and likely benefit plants by attracting seed dispersers (Cipollini 2000). However, they can also act inadvertently as feeding attractants (Table 1).

Apocarotenoids, such as α- and β-ionone (Fig. 1), have been shown to be strong attractants (Williams et al. 2000) or deterrents (Wei et al. 2011 and references therein) of phytophagous insects. α-ionone may act as an intraspecific aggregation cue produced by actively feeding insects, which by continuously crushing plant cells, may mix cytosolic carotenoid cleavage oxygenases (CCOs) with plastid-localized carotenoids or may directly degrade them with CCOs in their saliva (Heath et al. 2002; Rhainds et al. 2007). These CCOs are known to be much more active under high light conditions (Scherzinger and Al-Babili 2008), and diurnal phytophagous beetles require high light conditions to find mates (Heath et al. 2001). However, apocarotenoids can also be produced chemically under oxidizing conditions, that is, without the direct aid of enzymes (Stratton et al. 1993; Gessler et al. 2002; Walter and Strack 2011; Ramel et al. 2012). This is interesting as continuously damaged plant cells experience oxidizing conditions, and many plants generate singlet oxygen and other ROS with the aid of photosensitized allelochemicals (Ahmad and Pardini 1990).

Manipulation of plant chemistry with carotenoid-derived hormones

Mutualistic associations with microbes have likely played an important role in the phenomenal evolutionary and ecological success of insects (Moran 2002; Janson et al. 2008). Virtually, every insect species that has been examined closely has been found to be engaged in some form of microbial mutualism, most frequently in the form of gut-associated bacteria (e.g. Buchner 1965; Douglas 1998). However, insect–fungal symbioses are also widespread across many insect groups including beetles (Scolytinae: Bentz and Six 2006), ants (Formicidae: Mikheyev et al. 2006), moths (Tortricidae: Fermaud and Lemenn 1989) and flies (Borkent and Bissett 1985; Gagné 1989; Schiestl et al. 2006; Heath and Stireman 2010). In these associations, the insect typically benefits from using the fungus as a food source (Bissett and Borkent 1988; Cherrett et al. 1989; Farrell et al. 2001; Janson et al. 2009; Heath and Stireman 2010) in exchange for dispersing the fungus or promoting fungal outcrossing (Schiestl et al. 2006). Given the current understanding of the hormonal regulation of plant defence chemistry, the ability of microbes to synthesize plant hormones (Table 2), and the induction of certain defence pathways in plants by microbes and herbivores, the potential exists for cooperating organisms to short-circuit these pathways towards their mutual advantage. Carotenoid derivatives may provide a means for such manipulation.

There are six groups of plant hormones traditionally recognized. These are auxin, ethylene, cytokinins, gibberellins, abscisic acid (ABA) and brassinosteroids (Kende and Zeevaart 1997). Recently, strigolactones were added as a seventh class (Pichersky 2008). Two of these classes, ABA and strigolactones, are derived in part or in whole from carotenoid precursors, and additional uncharacterized carotenoid-derived plant hormones may also exist (Walter and Strack 2011; Ramel et al. 2012).

Strigolactones are biosynthesized via the oxidative breakdown of carotenoid precursors via carotenoid cleavage oxygenases (Matusova et al. 2005; Humphrey and Beale 2006; Humphrey et al. 2006; Lopez-Raez et al. 2008) and have been found in plant species from at least 13 different families (Awad et al. 2006; Bouwmeester et al. 2007; Steinkellner et al. 2007; Yoneyama et al. 2007a; Yoneyama et al. 2007b). Cook et al. (1972) identified strigol as a germination stimulant for the parasitic weeds in the genus *Striga,* and numerous subsequent studies have verified this (reviewed in Scholes and Press 2008). More recently, experiments have shown that the long sought after fungal branching factor associated with successful colonization by arbuscular mycorrhizal fungi is a strigolactone, 5-deoxystrigol (Fig. 2; Akiyama et al. 2005). Strigolactones are also the causal agent in prohibiting above-ground lateral branching in *Arabidopsis*, rice and pea, illustrating their importance to plant architecture (Gomez-Roldan et al. 2008; Umehara et al. 2008) and quite possibly its manipulation by galling insects.

ABA is synthesized in plants from carotenoid precursors via a carotenoid cleavage oxygenase (Schwartz and Zeevaart 2004; Wasilewska et al. 2008). Interestingly, many fungi also have the ability to produce ABA (Table 2), but it appears that they use the mevalonic acid pathway and not carotenoid precursors (Schwartz and Zeevaart 2004). ABA plays a central role in seed development, stomatal regulation and plant responses to abiotic stressors such as osmotic, drought and possibly cold stress (Assmann 2004; Finkelstein 2004; Yamaguchi-Shinozaki and Shinozaki 2006); evidence is mounting that ABA is also centrally involved in regulating responses to biotic stressors (Anderson et al. 2004).

It is well established that plants react to biotic stresses such as viruses, bacteria, fungi and herbivorous insects by up-regulating defensive pathways (Mauch-Mani and Mauch 2005). These induced defences are regulated by two major biochemical signalling pathways: the salicylic acid (SA) pathway and the jasmonic acid/ethylene (JA) pathway (Spoel et al. 2003). When a plant is attacked, either the SA or JA pathway is induced, but generally not both. This is because the pathways can be reciprocally inhibitory (Kunkel and Brooks 2002; Cipollini et al. 2004; Lorenzo and Solano 2005). Furthermore, ABA can negatively interact with both the SA and JA pathways (reviewed by Lorenzo and Solano 2005; Mauch-Mani and Mauch 2005; Fujita et al. 2006; Asselbergh et al. 2008), thus playing a central role in regulating plant responses to both abiotic and biotic plant stresses. It is known that environmental conditions that induce increases in plant ABA levels (e.g. drought) enhance disease susceptibility in some pathosystems (e.g. Ma et al. 2001; Mayek-Perez et al. 2002; Koga et al. 2004; Garrett et al. 2006). Positive relationships between drought and disease severity may be related to the negative effect of ABA on biotic stress signalling. However, this response may not be universal as the severity of pathogen attack can also be negatively correlated with drought stress (Achuo et al. 2006; Enright and Cipollini 2011). However, directly increasing plant levels of ABA (either by exogenous application or via mutant plants) has been shown to negatively affect disease resistance in a number of studies (Henfling et al. 1980; Salt et al. 1986; Ward et al. 1989; McDonald and Cahill 1999; Audenaert et al. 2002; Mohr and Cahill 2003; Thaler and Bostock 2004; Mohr and Cahill 2007).

Studies supporting a negative relationship between ABA and plant resistance continue to accumulate. This opens the possibility that microbes or other plant-feeding organisms could manipulate their hosts through hormonal interference; however, documentation that microorganisms produce

Table 2 An abbreviated list of fungi known to produce carotenoids or abscisic acid

Genus	Division[a]	Class	Order	Family	Carotenoid biosynthesis	ABA biosynthesis	References[b]
Neurospora	A	Ascomycetes	Sordariales	Sordariaceae	Yes		1
Cercospora	A	Dothideomycetes	Capnodiales	Mycosphaerellaceae	Yes	Yes	2,3,4
Septoria	A	Dothideomycetes	Capnodiales	Mycosphaerellaceae		Yes	5
Macrophoma	A	Dothideomycetes	Dothideales	Botryosphaeriaceae		Yes	6
Botryosphaeria	A	Dothideomycetes	Dothideales	Botryosphaeriaceae			
Stagonospora	A	Dothideomycetes	Pleosporales	Phaeosphaeriaceae		Yes	5
Alternaria	A	Dothideomycetes	Pleosporales	Pleosporaceae		Yes	4,7
Erysiphe	A	Leotiomycetes	Erysiphales	Erysiphaceae			
Sclerotinia	A	Leotiomycetes	Helotiales	Sclerotiniaceae	Trace		8
Botrytis	A	Leotiomycetes	Helotiales	Sclerotiniceae	Trace	Yes	9,10,11
Monilia	A	Leotiomycetes	Helotiales	Sclerotiniceae		Yes	12
Cytospora	A	Sordariomycetes	Diaporthales	Valsaceae		Yes	12
Fusarium	A	Sordariomycetes	Hypocreales	Nectriaceae		Yes	11
Ceratocystis	A	Sordariomycetes	Microascales	Ceratocystidaceae		Yes	11
Agrocybe	B	Agaricomycetes	Agaricales	Bolbitiaceae		Yes	4
Coprinus	B	Agaricomycetes	Agaricales	Agaricaceae		Yes	4
Trametes	B	Agaricomycetes	Poriales	Poriceae		Yes	4
Sclerotium	B	Basidiomycetes	Agaricales	Typhulaceae	Yes		13
Polyporus	B	Basidiomycetes	Polyporales	Polyporaceae		Yes	4
Rhizoctonia	B	Basidiomycetes	Polyporales	Corticiaceae		Yes	11
Blakeslea	Z	Zygomycetes	Mucorales	Choanephoraceae	Yes		1
Phycomyces	Z	Zygomycetes	Mucorales	Mucoraceae	Yes		1
Mucor	Z	Zygomycetes	Mucorales	Mucoraceae	Yes	Yes	1,4
Rhizopus	Z	Zygomycetes	Mucorales	Mucoraceae	Yes	Yes	1,4
Absidia	Z	Zygomycetes	Mucorales	Mucoraceae	Yes		1
Parasitella	Z	Zygomycetes	Mucorales	Mucoraceae	Yes		1,14
Cunninghamella	Z	Zygomycetes	Mucorales	Cunninghamellaceae		Yes	4

Cells without information are not necessarily negative; the information may have been overlooked by the authors

[a] Division is either Ascomycota (A), Basidiomycota (B) or Zygomycota (Z)

[b] References: (1) Burmester et al. 2007; (2) Inomata et al. 2004a; (3) Schmidt et al. 2008; (4) Crocoll et al. 1991; (5) Vasyuk et al. 1996; (6) Arai et al. 1989; (7) Dahiya et al. 1988; (8) Georgiou et al. 2001a, Zervoudakis et al. 2003; (9) Inomata et al. 2004b; (10) Kettner and Dorffling 1995; (11) Dorffling et al. 1984; (12) Vizarova et al. 1997; (13) Georgiou 1997, Georgiou et al. 2001b; (14) Schimek and Wöstemeyer 2006

ABA at the infection site or actively regulate its level in plants are lacking. To our knowledge, only Kettner and Dorffling (1995) have shown unequivocally that fungus-derived ABA can explain variation in plant levels of ABA during the infection process of tomato plants by *Botrytis* fungi.

One of the few studies to evaluate the effects of ABA on both pathogens and insect herbivores found that ABA-deficient tomato mutants had lower levels of disease caused by *Pseudomonas syringae*, but supported higher growth rates of *Spodoptera exigua* larvae than control plants (Thaler and Bostock 2004). The mutants also showed higher levels of the SA-inducible PR4 gene, which likely contributed to the observed increase in pathogen resistance. The potential for cross-talk among these defensive pathways provides an opportunity for the evolution of mutualistic associations between biotrophic pathogens and insects; for instance, herbivore feeding could induce the JA pathway; thus, down-regulating the SA pathway or pathogens could induce the SA pathway, down-regulating the JA pathway. Alternatively, herbivore production of ABA could modulate the interaction between the JA and SA pathways as suggested by the results of Thaler and Bostock (2004).

We have recently found carotenoids and ABA in the salivary glands of the Ambrosia galler *Asteromyia carbonifera* in concentrations well above those required for physiological effects on the plant (Heath et al. 2012). Many cecidomyiids, including *A. carbonifera,* have obligate fungal symbionts. This hormone may be instrumental in allowing growth of their symbiotic fungus, which forms the gall structure and is their primary food source (Janson et al. 2009; Heath and Stireman 2010). As with other systems in which larvae have glandular carotenoids (Eichenseer et al. 2002; Sakudoh et al. 2007), understanding the ecological trade-offs is key to ascribing a role for these compounds.

Carotenoids in insect-enemy and tritrophic interactions

Aposematic and cryptic colouration

Because carotenoids generally must be obtained from the environment and may be limiting, access to carotenoids may influence insect population dynamics and niche evolution via their effects on susceptibility to enemies and presumably mate choice (see also the section 'Resource signalling: odour'). Carotenoid pigmentation is correlated with levels of toxic defensive compounds and can function as precursors to these compounds, such as the predator-repellent grasshopper ketone (Fig. 2; Meinwald et al. 1968). Carotenoids can underlie not only yellow, orange or red colouration, but also green (in some insects) and purple–blue (in other arthropods) when combined with specific carotenoproteins or chlorophyll degradation products such as pterobilin. Carotenoproteins anchor the carotenoids in specific configurations that change the spectral qualities of the chromophore and allow the absorption of light in uncharacteristic regions of the visible spectrum (Britton and Helliwell 2008).

Aphids are known to derive body colour from carotenoids and frequently exhibit intraspecific colour morphs (Losey et al. 1997). Most insects are thought to obtain carotenoids from their diets; however, aphids are phloem feeders and the carotenoid concentration in phloem is expected to be low (Czeczuga 1976). Several studies have shown the presence of torulene, a red carotenoid, in aphid and katydid colour morphs. Torulene is rare in plants and it is hypothesized to be biosynthesized by symbiotic microbes (Weisgraber et al. 1971; Britton et al. 1977; Jenkins et al. 1999), but may be derived from laterally transferred fungal genes in some insects (Moran and Jarvik 2010). Carotenoid-derived colours can have substantial ecological consequences in aphids and butterflies (Gerould 1921); for instance, Losey et al. (1997) found that the maintenance of a red–green colour polymorphism in the pea aphid was regulated by differential predation and parasitism. These opposing forces result in equilibrium between the red and green morphs. Frequency-dependent selection, mediated by parasitoid learning, can also result in equilibrium between the aphid colour morphs (Langley et al. 2006), and recent studies indicate that increased light can induce a much darker colour morph even *within* a clone (Alkhedir et al. 2010). Whether these aphid colour morphs represent some form of crypsis or aposematism has not been determined.

For signals to evolve and persist, they must be honest (Zahavi 1975) *or* be augmented by a high frequency of honest models in their environment. Current theory and evidence indicate that mate signalling traits should be strongly correlated with individual health and condition (Berglund et al. 1996), but not necessarily genetically linked or even under direct genetic control (Kodric-Brown and Brown 1984; Sandre et al. 2007). And, Badyaev et al. (2001) illustrate that carotenoid-based plumage in birds is actually a complex, composite representation of several aspects of individual condition, which suggests the existence of physiological or developmental trade-offs. The physiological connection between carotenoids and protection from autotoxicity, immunity, biosynthesis of defence (e.g. smaller terpenes) and antioxidant capacity may make them particularly useful for colour signalling both within and between species (Blount et al. 2009), but in insects, the expected physiological trade-offs have not been forthcoming (Sandre et al. 2007). Nevertheless, correlations between colouration and defensive traits have been found. The bright red, carotenoid-derived elytral colouration of many ladybird beetles has the potential to signal honestly the level of beetle toxicity to potential predators (Bezzerides et al. 2007). Upon attack by predators, *Harmonia axyridis* ladybird beetles react with reflexive bleeding and release the defensive alkaloid harmonine, the concentration of which is significantly correlated with the proportion of elytra area that is red (Bezzerides et al. 2007). Aposematic colouration is also correlated with carotenoid concentration in *Leptinotarsa* leaf beetles that appear to sequester carotenoids from their host plants (Poff 1976). Carotenoids have been found in whole-body and hair-tuft extracts of a number of aposematic Lepidoptera species (Sandre et al. 2007; Blount and McGraw 2008), including monarch butterflies where it is responsible for the dramatic yellow striping of caterpillars (Rothschild et al. 1978). Several aposematically coloured butterflies exhibit levels of carotenoids that correlate positively with toxic prooxidant compounds, suggesting that carotenoids may protect susceptible tissues from autotoxicity as well as provide warning colouration (Rothschild et al. 1986; Nishida et al. 1994). Interestingly, in butterfly systems involving mimicry, mimics consistently have lower carotenoid concentrations than their models. This pattern does not hold up in the classic monarch-viceroy batesian mimicry (Rothschild et al. 1986) and may have led Ritland and Brower (1991) to re-examine and ultimately reverse our understanding of this classical mimicry system (Rothschild 1991).

In insects, blue pigments such as pterobilins can combine with carotenoids to yield cryptic colouration (Rothschild and Mummery 1985). Larvae of the butterfly, *Colias philodice*, and the stick insect *Dixippus morosus* both combine carotenes with unknown blue pigments to achieve a green colour (Fox 1976). Many lepidopteran larvae are also coloured green by the physical mixing of blue chlorophyll degradation products and carotenoids (Rothschild and Mummery 1985). Furthermore, the intensity of the green colour is correlated with carotenoid concentration (Grayson et al. 1991). Interestingly, some of these cryptic larvae have elaborate polyphenisms that allow them to alter their colouration over the course of larval development to match the colour of their environment (Grayson and Edmunds 1989; Noor et al. 2008). This response can be triggered by the quality of the diet (Greene 1996) and/or by the quality of light perceived by the larvae (Grayson and Edmunds 1989; Noor et al. 2008) and appears to be adaptive (Edmunds and Grayson 1991).

These systems seem ideally suited for the investigation of genetic assimilation as some of the species in these groups appear to be relatively fixed for certain colour morphs that may have been derived from ancestors with flexible polyphenisms. Genetic assimilation purports to explain how polyphenisms can become fixed in populations and thus facilitate speciation and niche specialization. Although Grayson and Edmunds (1989) allude to this concept, they do not expound on its potential importance. The power of genetic assimilation to facilitate speciation comes from the conditional ratchet effect (reviewed by West-Eberhard 2003) that polyphenisms can have on natural selection, that is, because a particular polyphenism is generally only expressed under conditions in which it is likely to be beneficial, natural selection tends to select for a lower induction threshold for that trait. Therefore, any expressed polyphenisms with an equal or lower induction threshold (i.e. genetically controlled) are more likely to show up in the next generation. Given the right environmental conditions, this process can produce a more-or-less fixed trait (West-Eberhard 2003). Interestingly, threshold evolution has been documented in dung beetles where expression of horned males is ultimately controlled by size and proximately controlled by the terpenoid, juvenile hormone (Moczek and Nijhout 2002).

Tritrophic signalling

One interesting phenomenon observed frequently in the studies of plant–arthropod interactions is a decrease in chlorophyll and carotenoids in *uninfested* tissues of plants *infested* with phytophages. This chlorosis occurs locally at the feeding site (Mothes and Seitz 1982; Hildebrand et al. 1986b; Ni et al. 2002; Heng-Moss et al. 2003), but also within undamaged tissue remote from the feeding site (Schuster et al. 1990; McAuslane et al. 2004). Numerous studies have also demonstrated ultrastructural changes in chloroplasts associated with plant cells near feeding sites, which seems to correspond to a decrease in the quantity of pigments in these cells (Oliveira et al. 2011) as well as starch grains. This is especially true for pathogen-infected cells (Camp 1981; Rey 1992) and the nutritive cells induced by galling insects (Birch et al. 1992; Bronner 1992; Rey 1992; Westphal 1992; Oliveira et al. 2011), but also of cells near caterpillar feeding sites (Maffei et al. 2004). The ultimate fate of the chlorophyll and carotenoids associated with chlorosis and major changes in chloroplasts has not been studied. However, the higher activity of prooxidant enzymes in these cells (Hildebrand et al. 1986a) may result in significant releases of volatile apocarotenoids (Salt et al. 1986; Fig. 2).

Given that many hymenopterans respond to volatile apocarotenoids (Table 1) and that insect feeding is associated with chlorosis, it is surprising that the recent proliferation of plant studies on systemically inducible volatile organic compounds (VOCs), which can attract parasitoid wasps, (reviewed in Arimura et al. 2005) has failed to identify any obvious volatile apocarotenoids associated with insect feeding. Although systemic decreases in chlorophyll and carotenoid content have been observed in damaged plants (McAuslane et al. 2004), studies indicating local decreases (i.e. near the feeding site) are more prevalent and more intense. It is possible that volatile apocarotenoids are released at the feeding site, but that inducible, systemically released volatile organic compounds obscure detection of locally released apocarotenoids. Indeed, it is not uncommon to find parasitoid studies with lists of unidentified electroantennographically active compounds that are either masked by larger peaks or are undetectable by gas chromatography (e.g. Gouinguene et al. 2005). Most studies involving systemically induced volatile emission have measured the volatiles from whole plants; few studies have concentrated on the volatiles emitted only from the feeding site. Coleman et al. (1997) showed that the parasitoid *Cotesia glomerata* can distinguish between feeding sites of *Pieris brassicae* larvae on *Brassica oleracea* with stronger attraction to larvae feeding on the top most leaves. They also illustrated that the parasitoids were unable to distinguish between infested and unifested plants when the larvae were feeding on lower leaves. Tissue age and environment can influence leaf carotenoid concentration and may explain the lack of attractiveness of larvae feeding on lower leaves (Feltwell and Valadon 1974; Rothschild et al. 1986; Norman et al. 1990; Hartel and Grimm 1998). For example, *B. oleracea* core tissue with limited light exposure has up to 30-fold less carotenoid than light-exposed tissues (Bondi and Meyer 1946).

If apocarotenoids are in fact important volatile cues for natural enemies, they are more likely to be discovered by comparing systemically released volatiles with those emanating from local feeding sites. Theoretically, the volatiles emitted from local feeding sites are predicted to be more important in natural enemy attraction than those released systematically both from a behavioural and a plant physiological perspective. Therefore, a renewed focus on the volatiles specifically associated with the feeding site could provide better natural enemy attractants as well as test the presence of apocarotenoids.

The quantity of volatiles emitted from a local feeding site will be much lower than those released systemically simply because of the reduction in tissue involved. However, from a behavioural perspective, this is not likely to present a problem for predators and parasitoids. Insects are known to be highly sensitive to volatile compounds. Workers have shown that a single odour molecule is sufficient to evoke a nerve impulse (Kaissling 1996), and semiochemicals often have extremely high physiological activity at levels so low as to be nearly undetectable by even the most sensitive of chromatographic equipment (e.g. femtogram levels, Heath et al. 2005). Furthermore, volatiles emanating from a point source are far more useful as odour cues than broadly emitted sources. In fact, male moths flying in a homogenous cloud of female pheromone behave as if they were flying in clean air (Baker 1985). This is due to the physiological and behavioural mechanisms of odour source perception and location in insects. Insects do not locate an odour source by flying up a concentration gradient, but rather by responding stereotypically to pulses or filaments of highly concentrated odour (see Baker and Vickers 1997 for a review of optomotor anemotaxis). Therefore, the volatiles emanating from a point source (e.g. the damaged site of an actively feeding herbivore) are likely to be more important in host location than those released systemically. Furthermore, studies have found that galling insects fail to induce the systemic release of volatile organic compounds that are typically thought to attract predators and parasitoids (Tooker and De Moraes 2007; Tooker and De Moraes 2008; Tooker et al. 2008), and detailed studies have shown a much more intense reduction in pigments near the feeding sites of galling insects (Oliveira et al. 2011 and references therein). Perhaps, the high parasitism rates experienced by many galling insects are based instead on visual or other locally emitted volatile cues.

Carotenoids are a huge reserve of precursors for volatile apocarotenoids that may prove to be important in the attraction of natural enemies to actively feeding hosts. That plants have evolved the ability to induce the production of VOCs for the sole purpose of attracting natural enemies is unlikely. We are not suggesting that natural enemies do not respond to these compounds or that plants do not benefit from attracting them, but rather that natural enemy attraction has been an epiphenomenon of plant defence, including autotoxic protection from their onslaught of prooxidant species. Provided that plants enjoy a fitness benefit from attracting natural enemies, they may have fine-tuned the release of volatiles, especially from the feeding site, over evolutionary time, to serve a secondary purpose of attracting carnivores. Furthermore, we predict that some of the most important volatiles are likely to be derived from carotenoid precursors. In fact, in the rapidly radiating complex of the nominal species *Asteromyia carbonifera* (Stireman et al. 2008; Janson et al. 2010; Stireman et al. 2010), we have found that the quality and quantity of adult accessory gland carotenoids is consistently gall-morphotype specific and correlates nearly perfectly with attack by an egg parasitoid both within and across morphotypes (Heath et al. 2012).

Conclusions

The ubiquity, physiological necessity, and varied functions of carotenoids and their derivatives across the tree of life suggest that they may also play significant roles in insect ecology and evolution, as limiting resources, as defensive or repellent compounds, and as signals or cues. In particular, emerging evidence of the roles of carotenoids as self-protective antioxidants, as precursors to plant hormones such as strigolactones and ABA, and as precursors to volatile apocarotenoids suggests that they may be important mediators of plant–insect, insect-mutualist and tritrophic interactions. Their potential as volatile chemical cues that parasitoids and other insects could use to find their herbivorous prey within the torrent of intermingling odours in nature is promising, but largely unexplored. The co-option of hormone derivatives of carotenoids suggests a novel way in which insects may manipulate plant growth and defence signalling pathways and conspire in mutualistic associations with microbes and fungi. The many critical roles of carotenoids in colouration, vision, diapause, photoperiodism, as antioxidants and as defence compounds suggest that they may often be a limiting resource for insects and therefore represent an important dimension of the ecological niches of many insect taxa. This would also suggest that insects should have fine-tuned systems for detecting and assessing carotenoid quality and quantity of their food, but this remains largely unexplored.

Research aimed at understanding the roles that carotenoids and their derivatives play in species interactions should have a multitrophic perspective starting first at the level of the primary producer and working up the food web to higher trophic levels. With this in mind, tracking the flow of major plant carotenoids (with the use of stable isotopes or radiolabelling) through herbivores and on to higher trophic levels would provide a framework for further assessing the relative contribution of maternal, dietary, symbiotic and potential de novo sources of insect carotenoids. At the plant level, the role of carotenoids in protecting plants from their own production of potentially autotoxic, photosensitized allelochemicals or ROS is largely unexplored and depending on the degree to which autotoxicity is a factor, carotenoids may modulate trade-offs between defence and other plant systems such as growth, photosynthesis or reproduction. This work would help place the plant within the emerging concept of universal adaptive strategy theory (Grime and Pierce 2012). At the herbivore level, carotenoids may protect against photosensitized plant allelochemicals either directly or via indirect protection of antioxidant enzymes, but work in this area is lacking in insects. As mating signals, carotenoids may provide both colour directly and odour via apocarotenoids, but the potential trade-offs here have not been assessed nor the degree to which carotenoid-based sexual selection is involved in the evolution of insect life history strategies. Probably, the most interesting and practical area for further study is with regard to the third trophic level. Apocarotenoids generated by the plant at the herbivore feeding site have great potential as cues to foraging parasitoids and predators of the presence of herbivores, but to our knowledge, this has not been explored nor has the impact of carotenoids on the immune response of the herbivore once it has been parasitized or infected. Finally, whether insect parasitoids, predators or herbivorous insects select food resources on the basis of carotenoid quality or quantity has not been addressed directly, but provides a clear and open direction for future research.

Understanding the roles of carotenoids in the evolutionary ecology of insects is a potentially rich field that promises to enrich our understanding of the chemical mediation of ecological interactions in nature and may provide excellent model systems for integrating aspects of organism development with current evolutionary theory (Badyaev 2011). In turn, understanding the factors that drive such phenomena as host-plant attractiveness or repellency to herbivores, pathogens and natural enemies; pollinator and seed-disperser attraction; and regulation of microbial symbionts has numerous applied implications.

Acknowledgments Jennifer L. Heath and several anonymous reviewers provided helpful comments on earlier versions of the manuscript. This work was supported by a National Science Foundation grant DEB-0614433 to JOS and the Wright State University Environmental Science PhD program.

References

Aarseth KA, Schram TA (2002) Susceptibility to ultraviolet radiation in *Calanus finmarchicus* and *Lepeophtheirus salmonis* and the adaptive value of external filtering (Crustacea : Copepoda). J Plankton Res 24:661–679

Achuo EA, Prinsen E, Hofte M (2006) Influence of drought, salt stress and abscisic acid on the resistance of tomato to *Botrytis cinerea* and *Oidium neolycopersici*. Plant Pathol 55:178–186

Ahmad S (1992) Biochemical defense of prooxidant plant allelochemicals by herbivorous insects. Biochem Syst Ecol 20: 269–296

Ahmad S, Pardini RS (1990) Mechanisms for regulating oxygen toxicity in phytophagous insects. Free Radic Biol Med 8: 401–413

Akiyama K, Matsuzaki K, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435:824–827

Alkhedir H, Karlovsky P, Vidal S (2010) Effect of light intensity on colour morph formation and performance of the grain aphid *Sitobion avenae* F (Homoptera: Aphididae). J Insect Physiol 56:1999–2005

Altincicek B, Kovacs JL, Gerardo NM (2011) Horizontally transferred fungal carotenoid genes in the two-spotted spider mite *Tetranychus urticae*. Biol Lett 00:1–5

Anderson JP, Badruzsaufari E, Schenk PM, Manners JM, Desmond OJ, Ehlert C, Maclean DJ, Ebert PR, Kazan K (2004) Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in Arabidopsis. Plant Cell 16:3460–3479

Andersson J, Borg-Karlson A, Vongvanich N, Wiklund C (2007) Male sex pheromone release and female mate choice in a butterfly. J Exp Biol 210:964–970

Aplin RT, Birch MC (1970) Identification of odorous compounds from male Lepidoptera. Experientia 26:1193–1194

Arai K, Shimizu S, Miyajima H, Yamamoto Y (1989) Castaneiolide, abscisic acid and monorden, phytotoxic compounds isolated from fungi (*Macrophoma castaneicola* and *Didymosporium radicicola*) cause black root rot disease in chestnut trees. Chem Pharm Bull 37:2870–2872

Archetti M (2000) The origin of autumn colours by coevolution. J Theor Biol 205:625–630

Arimura G, Kost C, Boland W (2005) Herbivore-induced, indirect plant defences. Biochim Biophys Acta Mol Cell Biol Lipids 1734:91–111

Asselbergh B, De Vieesschauwer D, Hofte M (2008) Global switches and fine-tuning—ABA modulates plant pathogen defense. Mol Plant Microbe Interact 21:709–719

Assmann SM (2004) Abscisic acid signal transduction in stomatal responses. In: Davies PJ (ed) Plant hormones biosynthesis, signal transduction, action! 3rd edn. Kluwer Academic Publishers, Boston, pp 391–412

Aucoin RR, Fields P, Lewis MA, Philogene BJR, Arnason JT (1990) The protective effect of antioxidants to a phototoxin-sensitive insect herbivore, *Manduca sexta*. J Chem Ecol 16:2913–2924

Aucoin R, Guillet G, Murray C, Philogene BJR, Arnason JT (1995) How do insect herbivores cope with the extreme oxidative stress of phototoxic host plants? Arch Insect Biochem Physiol 29:211–226

Audenaert K, De Meyer GB, Hofte MM (2002) Abscisic acid determines basal susceptibility of tomato to *Botrytis cinerea* and suppresses salicylic acid-dependent signaling mechanism. Plant Physiol 128:491–501

Auldridge ME, McCarty DR, Klee HJ (2006) Plant carotenoid cleavage oxygenases and their apocarotenoid products. Curr Opin Plant Biol 9:315–321

Awad AA, Sato D, Kusumoto D, Kamioka H, Takeuchi Y, Yoneyama K (2006) Characterization of strigolactones, germination stimulants for the root parasitic plants *Striga* and *Orobanche*, produced by maize, millet and sorghum. Plant Growth Regul 48: 221–227

Babin A, Biard C, Moret Y (2010) Dietary supplementation with carotenoids improves immunity without increasing its cost in a crustacean. Am Nat 176:234–241

Badyaev AV (2011) Origin of the fittest: link between emergent variation and evolutionary change as a critical question in evolutionary biology. Proc R Soc B 278:1921–1929

Badyaev AV, Hill GE, Dunn PO, Glen JC (2001) Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. Am Nat 158:221–235

Baker TC (1985) Chemical control of behavior. In: Kerkut GA, Gilbert LI (eds) Behavior, vol 9, comprehensive insect physiology, biochemistry, and pharmacology, vol 9. Pergamon Press, Oxford, pp 621–672

Baker TC, Vickers NJ (1997) Pheromone-mediated flight in moths. In: Carde RT, Minks AK (eds) Insect pheromone research: new directions. Chapman & Hall, New York, pp 248–264

Baldermann S, Naim M, Fleischmann P (2005) Enzymatic carotenoid degradation and aroma formation in nectarines (*Prunus persica*). Food Res Int 38:833–836

Bartram S, Jux A, Gleixner G, Boland W (2006) Dynamic pathway allocation in early terpenoid biosynthesis of stress-induced lima bean leaves. Phytochemistry 67:1661–1672

Bentz BJ, Six DL (2006) Ergosterol content of fungi associated with *Dendroctonus ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). Ann Entomol Soc Am 99:189–194

Berenbaum MR (1987) Charge of the light brigade: phototoxicity as a defense against insects. ACS Symp Ser 339:206–216

Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biol J Linn Soc 58:385–399

Bezzerides AL, McGraw KJ, Parker RS, Husseini J (2007) Elytra color as a signal of chemical defense in the Asian ladybird beetle *Harmonia axyridis*. Behav Ecol Sociobiol 61:1401–1408

Bhosale P, Bernstein PS (2007) Vertebrate and invertebrate carotenoid-binding proteins. Arch Biochem Biophys 458:121–127

Bi JL, Felton GW (1995) Foliar oxidative stress and insect herbivory—primary compounds, secondary metabolites, and reactive oxygen species as components of induced resistance. J Chem Ecol 21:1511–1530

Birch M (1970) Pre-courtship use of abdominal brushes by nocturnal moth, *Phlogophora meticulosa* (L.) (Lepidoptera-Noctuidae). Anim Behav 18:310–316

Birch ML, Brewer JW, Rohfritsch O (1992) Biology of *Dasineura affinis* Cecidomyiidae and influence of its gall on *Viola odorata*. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 174–184

Bissett J, Borkent A (1988) Ambrosia galls: the significance of fungal nutrition in the evolution of the Cecidomyiidae. In: Pirozynski KA, Hawksworth DL (eds) Coevolution of fungi with plants and animals. Academic Press, San Diego, CA, pp 203–225

Blount JD, McGraw KJ (2008) Signal functions of carotenoid colouration. In: Britton G, LiaaenJensen S, Pfander H (eds) Carotenoids, vol 4: natural functions. Birkhäuser Verlag, Boston, pp 213–236

Blount JD, Speed MP, Ruxton GD, Stephens PA (2009) Warning displays may function as honest signals of toxicity. Proc R Soc B 276:871–877

Bondi A, Meyer H (1946) Carotene in Palestinian crops. J Agric Sci 36:1–5

Borkent A, Bissett J (1985) Gall midges (Diptera: Cecidomyiidae) are vectors of their fungal symbionts. Symbiosis 1:185–194

Bouvier F, Isner JC, Dogbo O, Camara B (2005) Oxidative tailoring of carotenoids: a prospect towards novel functions in plants. Trends Plant Sci 10:187–194

Bouwmeester HJ, Roux C, Lopez-Raez JA, Becard G (2007) Rhizosphere communication of plants, parasitic plants and AM fungi. Trends Plant Sci 12:224–230

Bradshaw HD, Schemske DW (2003) Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. Nature 426:176–178

Britton G (1995a) Structure and properties of carotenoids in relation to function. Faseb J 9:1551–1558

Britton G (1995b) Chapter 7: worked examples of isolation and analysis, example 1, higher plants. In: Britton G, Liaaen-Jensen S, Pfander H (eds) Carotenoids, volume 1A: isolation and analysis. Birkhäuser Verlag, Boston, MA, pp 201–214

Britton G (2008) Chapter 15: functions of carotenoid metabolites and breakdown products. In: Britton G, Liaaen-Jensen S, Pfander H (eds) Carotenoids, volume 4: natural functions. Birkhäuser Verlag, Boston, pp 309–323

Britton G, Helliwell JR (2008) Chapter 6: carotenoid-protein interactions. In: Britton G, Liaaen-Jensen S, Pfander H (eds) Carotenoids, volume 4: natural functions. Birkhäuser Verlag, Boston, pp 99–117

Britton G, Lockley WJS, Harriman GA, Goodwin TW (1977) Pigmentation of ladybird beetle *Coccinella septempunctata* by carotenoids not of plant origin. Nature 266:49–50

Britton G, Liaaen-Jensen S, Pfander H (2004) Carotenoids handbook. Birkhäuser Verlag, Boston, MA

Bronner R (1992) The role of nutritive cells in the nutrition of cynipids and cecidomyiids. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 118–140

Buchner P (1965) Endosymbiosis of animals with plant microorganisms. Wiley Interscience, New York

Burmester A, Richter M, Schultze K, Voelz K, Schachtschabel D, Boland W, Woestemeyer J, Schimek C (2007) Cleavage of beta-carotene as the first step in sexual hormone synthesis in zygomycetes is mediated by a trisporic acid regulated beta-carotene oxygenase. Fungal Genet Biol 44:1096–1108

Camp RR (1981) Insect fungus blister galls on *Solidago graminifolia* and *Solidago rugosa*.1. A macroscopic and light microscopic study of the host-parasite relationship. Can J Bot 59:2466–2477

Carroll MJ, Berenbaum MR (2006) Lutein sequestration and furanocoumarin metabolism in parsnip webworms under different ultraviolet light regimes in the montane west. J Chem Ecol 32:277–305

Carroll M, Hanlon A, Hanlon T, Zangerl AR, Berenbaum MR (1997) Behavioral effects of carotenoid sequestration by the parsnip webworm, *Depressaria pastinacella*. J Chem Ecol 23:2707–2719

Catoni C, Peters A, Schaefer HM (2008) Life history trade-offs are influenced by the diversity, availability and interactions of dietary antioxidants. Anim Behav 76:1107–1119

Cherrett JM, Powell RJ, Stradling DJ (1989) The mutualism between leaf-cutting ants and their fungus. In: Wilding N, Collins NM, Hammond PM, Webber JF (eds) Insect-fungus interactions. Academic Press, New York, pp 93–116

Cipollini ML (2000) Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. Rev Chil Hist Nat 73:421–440

Cipollini D, Enright S, Traw MB, Bergelson J (2004) Salicylic acid inhibits jasmonic acid-induced resistance of *Arabidopsis thaliana* to *Spodoptera exigua*. Mol Ecol 13:1643–1653

Coleman RA, Barker AM, Fenner M, King FC (1997) Relative effect of different host feeding site on long-range host location and electroantennogram response in the parasitoid *Cotesia glomerata* (Hym., Braconidae). J Appl Entomol 121:487–494

Cook CE, Coggon P, Mcphail AT, Wall ME, Whichard LP, Egley GH, Luhan PA (1972) Germination stimulants. II. Structure of strigol—potent seed-germination stimulant for witchweed (*Striga lutea* Lour.). J Am Chem Soc 94:6198–6199

Cornet S, Biard C, Moret Y (2007) Is there a role for antioxidant carotenoids in limiting self-harming immune response in invertebrates? Biol Lett 3:284–288

Crocoll C, Kettner J, Dorffling K (1991) Abscisic acid in saprophytic and parasitic species of fungi. Phytochemistry 30:1059–1060

Czeczuga B (1976) Investigations on the carotenoids in 19 species of aphids and their host plants. Zool Pol 25:27–46

Czeczuga B (1980) Investigations on carotenoids in insects. I. The presence and metabolism of carotenoid pigments in the aphids. Rocz Akad Med Im Juliana Marchlewskiego Bialymst 25:113–120

Czeczuga B (1981) Investigations on carotenoids in insects. 4. The occurrence of particular carotenoids in *Apis melifera* L (Apidae). Apidologie 12:107–112

Czeczuga B (1982) Investigations on carotenoids in insects.6. Occurrence of alpha-doradexanthin in some Insects. Folia Biol (Krakow, Pol) 30:143–148

Czeczuga B (1985) Investigations on carotenoids in insects. 7. Contents of carotenoids in worker bees feeding on flowers of different plants. Zool Pol 32:183–190

Czeczuga B (1986) Investigations on carotenoids in insects. 8. The presence of carotenoids in various species of Lepidoptera. Biochem Syst Ecol 14:345–351

Czeczuga B (1988) Investigations on carotenoids in insects. 9. Apocarotenals in representatives of the Cerambycidae family. Folia Biol (Krakow, Pol) 36:167–172

Czeczuga B (1990) Investigations on carotenoids in insects. 10. Changes in the carotenoids in butterflies (Lepidoptera). Folia Biol (Krakow, Pol) 38:5–12

Czeczuga B (1991) Investigations on insects. 11. Carotenoids in some cave-dwelling insects. Folia Biol (Krakow, Pol) 39:17–20

Czeczuga B, Mironiuk W (1980) Investigations on carotenoids in insects. 2. Water insects. Acta Hydrobiol 22:29–36

Czeczuga B, Weyda F (1982) Investigation on carotenoids in insects. 5. Archaeognatha Insecta Apterygota. Zool Pol 29:23–32

Dahiya JS, Tewari JP, Woods DL (1988) Abscisic acid from *Alternaria brassicae*. Phytochemistry 27:2983–2984

Davidson BS, Eisner T, Meinwald J (1991) 3,4-Didehydro-beta, beta-caroten-2-one, a new carotenoid from the eggs of the stick insect *Anisomorpha buprestoides*. Tetrahedron Lett 32:5651–5654

Davis AK, Cope N, Smith A, Solensky MJ (2007) Wing color predicts future mating success in male monarch butterflies. Ann Entomol Soc Am 100:339–344

De Moraes CM, Lewis WJ, Pare PW, Alborn HT, Tumlinson JH (1998) Herbivore-infested plants selectively attract parasitoids. Nature 393:570–573

Demmig-Adams B, Adams WW (1996) The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci 1:21–26

Dorffling K, Petersen W, Sprecher E, Urbasch I, Hanssen HP (1984) Abscisic acid in phytopathogenic fungi of the genera *Botrytis*, *Ceratocystis*, *Fusarium*, and *Rhizoctonia*. Z Naturforsch, C: J Biosci 39:683–684

Douglas AE (1998) Nutritional interactions in insect-microbial symbioses: aphids and their symbiotic bacteria *Buchnera*. Annu Rev Entomol 43:17–37

Dudareva N, Negre F, Nagegowda DA, Orlova I (2006) Plant volatiles: recent advances and future perspectives. Crit Rev Plant Sci 25:417–440

Dyer AG, Whitney HM, Arnold SEJ, Glover BJ, Chittka L (2007) Mutations perturbing petal cell shape and anthocyanin synthesis influence bumblebee perception of *Antirrhinum majus* flower colour. Arthropod Plant Interact 1:45–55

Edmunds M, Grayson J (1991) Camouflage and selective predation in caterpillars of the poplar and eyed hawkmoths (*Laothoe populi* and *Smerinthus ocellata*). Biol J Linn Soc 42:467–480

Eichenseer H, Murphy JB, Felton GW (2002) Sequestration of host plant carotenoids in the larval tissues of *Helicoverpa zea*. J Insect Physiol 48:311–318

Eisenreich W, Rohdich F, Bacher A (2001) Deoxyxylulose phosphate pathway to terpenoids. Trends Plant Sci 6:78–84

El-Sayed AM (2011) The pherobase: database of insect pheromones and semiochemicals. http://www.pherobase.com. Accessed 12 Mar 2012

Enright S, Cipollini D (2011) Overlapping defense responses to water limitation and pathogen attack and their consequences for resistance to powdery mildew disease in garlic mustard, *Alliaria petiolata*. Chemoecology 21:89–98

Escobar JA, Rubio MA, Lissi EA (1996) SOD and catalase inactivation by singlet oxygen and peroxyl radicals. Free Radical Biol Med 20:285–290

Farrell BD, Sequeira AS, O'Meara BC, Normark BB, Chung JH, Jordal BH (2001) The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). Evolution 55:2011–2027

Felton GW, Summers CB (1995) Antioxidant systems in insects. Arch Insect Biochem Physiol 29:187–197

Feltwell J, Rothschild M (1974) Carotenoids in 38 species of Lepidoptera. J Zool 174:441–465

Feltwell JS, Valadon LRG (1974) Carotenoid changes in *Brassica oleracea* var. *capitata* L. with age, in relation to large white butterfly, *Pieris brassicae* L. J Agric Sci 83:19–26

Fermaud M, Lemenn R (1989) Association of *Botrytis cinerea* with grape berry moth larvae. Phytopathology 79:651–656

Ferreira ACS, Monteiro J, Oliveira C, Pinho PG (2008) Study of major aromatic compounds in Port wines from carotenoid degradation. Food Chem 110:83–87

Finkelstein RR (2004) The role of hormones during seed development and germination. In: Davies PJ (ed) Plant hormones biosynthesis, signal transduction, action!, 3rd edn. Kluwer Academic Publishers, Boston, pp 513–537

Fox DL (1976) Animal biochromes and structural colours. University of California Press, Los Angeles

Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol 9:436–442

Gagné RJ (1989) The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY

Gao HY, Zhu HL, Shao Y, Chen AJ, Lu CW, Zhu BZ, Luo YB (2008) Lycopene accumulation affects the biosynthesis of some carotenoid-related volatiles independent of ethylene in tomato. J Integr Plant Biol 50:991–996

Garcia-Limones C, Schnabele K, Blanco-Portales R, Bellido ML, Caballero JL, Schwab W, Munoz-Blanco J (2008) Functional characterization of FaCCD1: a carotenoid cleavage dioxygenase from strawberry involved in lutein degradation during fruit ripening. J Agric Food Chem 56:9277–9285

Garrett KA, Dendy SP, Frank EE, Rouse MN, Travers SE (2006) Climate change effects on plant disease: genomes to ecosystems. Annu Rev Phytopathol 44:489–509

Gebbinck EAK, Jansen BJM, de Groot A (2002) Insect antifeedant activity of clerodane diterpenes and related model compounds. Phytochemistry 61:737–770

Georgiou CD (1997) Lipid peroxidation in *Sclerotium rolfsii*: a new look into the mechanism of sclerotial biogenesis in fungi. Mycol Res 101:460–464

Georgiou CD, Tairis N, Polycratis A (2001a) Production of beta-carotene by *Sclerotinia sclerotiorum* and its role in sclerotium differentiation. Mycol Res 105:1110–1115

Georgiou CD, Zervoudakis G, Tairis N, Kornaros M (2001b) Beta-carotene production and its role in sclerotial differentiation of *Sclerotium rolfsii*. Fungal Genet Biol 34:11–20

Gerould JH (1921) Blue-green caterpillars: the origin and ecology of a mutation in hemolymph color in *Colias* (*Eurymus*) *philodice*. J Exp Zool 34:385–415

Gessler NN, Sokolov AV, Belozerskaya TA (2002) Initial stages of trisporic acid synthesis in *Blakeslea trispora*. Appl Biochem Microbiol 38:536–543

Goff SA, Klee HJ (2006) Plant volatile compounds: sensory cues for health and nutritional value? Science 311:815–819

Gomez-Roldan V, Fermas S, Brewer PB, Puech-Pages V, Dun EA, Pillot JP, Letisse F, Matusova R, Danoun S, Portais JC, Bouwmeester H, Becard G, Beveridge CA, Rameau C, Rochange SF (2008) Strigolactone inhibition of shoot branching. Nature 455:189–194

Goodwin TW (1986) Metabolism, nutrition, and function of carotenoids. Annu Rev Nutr 6:273–297

Gouinguene S, Pickett JA, Wadhams LJ, Birkett MA, Turlings TCJ (2005) Antennal electrophysiological responses of three parasitic wasps to caterpillar-induced volatiles from maize (*Zea mays mays*), cotton (*Gossypium herbaceum*), and cowpea (*Vigna unguiculata*). J Chem Ecol 31:1023–1038

Grayson J, Edmunds M (1989) The causes of color and color change in caterpillars of the poplar and eyed hawkmoths (*Laothoe populi* and *Smerinthus ocellata*). Biol J Linn Soc 37:263–279

Grayson J, Edmunds M, Evans EH, Britton G (1991) Carotenoids and coloration of poplar hawkmoth caterpillars (*Laothoe populi*). Biol J Linn Soc 42:457–465

Greene E (1996) Effect of light quality and larval diet on morph induction in the polymorphic caterpillar *Nemoria arizonaria* (Lepidoptera: Geometridae). Biol J Linn Soc 58:277–285

Grime JP, Pierce S (2012) The evolutionary strategies that shape ecosystems. Wiley-Blackwell, New Jersey

Grunewald K, Hirschberg J, Hagen C (2001) Ketocarotenoid biosynthesis outside of plastids in the unicellular green alga *Haematococcus pluvialis*. J Biol Chem 276:6023–6029

Hamilton WD, Brown SP (2001) Autumn tree colours as a handicap signal. Proc R Soc B 268:1489–1493

Hartel H, Grimm B (1998) Consequences of chlorophyll deficiency for leaf carotenoid composition in tobacco synthesizing glutamate 1-semialdehyde aminotransferase antisense RNA: dependency on developmental age and growth light. J Exp Bot 49:535–546

Heath JJ, Stireman JO III (2010) Dissecting the association between a gall midge, *Asteromyia carbonifera*, and its symbiotic fungus, *Botryosphaeria dothidea*. Entomol Exp Appl 137:36–49

Heath JJ, Williams RN, Phelan PL (2001) High light intensity: a critical factor in the wind-tunnel flight of two scarabs, the rose chafer and Japanese beetle. J Chem Ecol 27:419–429

Heath JJ, Williams RN, Phelan PL (2002) Aggregation and male attraction to feeding virgin females in *Macrodactylus subspinosus* (F.) (Coleoptera: Scarabaeidae: Melolonthinae). Environ Entomol 31:934–940

Heath JJ, Zhang AJ, Roelofs WL, Smith RF (2005) Flight activity and further evidence for a female-produced sex pheromone of the apple leaf midge, *Dasineura mali*, in Nova Scotia. Northeast Nat 12:93–102

Heath JJ, Wells B, Cipollini D, Stireman III JO (2012) Carnivores and carotenoids are associated with adaptive behavioural divergence in a radiation of gall midges. Ecol Entomol. doi:10.1111/j.1365-2311.2012.01397.x

Henfling JWDM, Bostock RM, Kuc J (1980) Effect of abscisic acid on rishitin and lubimin accumulation and resistance to *Phytophthora infestans* and *Cladosporium cucumerinum* in potato-tuber tissue-slices. Phytopathology 70:1074–1078

Heng-Moss TM, Ni X, Macedo T, Markwell JP, Baxendale FP, Quisenberry SS, Tolmay V (2003) Comparison of chlorophyll and carotenoid concentrations among Russian wheat aphid (Homoptera: Aphididae)-infested wheat isolines. J Econ Entomol 96:475–481

Hildebrand DF, Rodriguez JG, Brown GC, Luu KT, Volden CS (1986a) Peroxidative responses of leaves in 2 soybean genotypes injured by 2-spotted spider mites (Acari, Tetranychidae). J Econ Entomol 79:1459–1465

Hildebrand DF, Rodriguez JG, Brown GC, Volden CS (1986b) 2-spotted spider mite (Acari, Tetranychidae) infestations on soybeans—effect on composition and growth of susceptible and resistant cultivars. J Econ Entomol 79:915–921

Hirschberg J (2001) Carotenoid biosynthesis in flowering plants. Curr Opin Plant Biol 4:210–218

Holopainen JK (2008) Importance of olfactory and visual signals of autumn leaves in the coevolution of aphids and trees. BioEssays 30:889–896

Humphrey AJ, Beale MH (2006) Strigol: biogenesis and physiological activity. Phytochemistry 67:636–640

Humphrey AJ, Galster AM, Beale MH (2006) Strigolactones in chemical ecology: waste products or vital allelochemicals? Nat Prod Rep 23:592–614

Ibdah M, Azulay Y, Portnoy V, Wasserman B, Bar E, Meir A, Burger Y, Hirschberg J, Schaffer AA, Katzir N, Tadmor Y, Lewinsohn E (2006) Functional characterization of CmCCD1, a carotenoid cleavage dioxygenase from melon. Phytochemistry 67:1579–1589

Inbar M, Izhaki I, Koplovich A, Lupo I, Silanikove N, Glasser T, Gerchman Y, Perevolotsky A, Lev-Yadun S (2010a) Why do many galls have conspicuous colours? An alternative hypothesis revisited conspicuous gall colors: a response to T. C. R. White. Arthropod Plant Interact 4:151–152

Inbar M, Izhaki I, Koplovich A, Lupo I, Silanikove N, Glasser T, Gerchman Y, Perevolotsky A, Lev-Yadun S (2010b) Why do many galls have conspicuous colors? A new hypothesis. Arthropod Plant Interact 4:1–6

Inomata M, Hirai N, Yoshida R, Ohigashi H (2004a) Biosynthesis of abscisic acid by the direct pathway via ionylideneethane in a fungus, *Cercospora cruenta*. Biosci Biotechnol Biochem 68: 2571–2580

Inomata M, Hirai N, Yoshida R, Ohigashi H (2004b) The biosynthetic pathway to abscisic acid via ionylideneethane in the fungus *Botrytis cinerea*. Phytochemistry 65:2667–2678

Janson EM, Stireman JO III, Singer MS, Abbot P (2008) Phytophagous insect-microbe mutualisms and adaptive evolutionary diversification. Evolution 62:997–1012

Janson EM, Grebenok RJ, Behmer ST, Abbot P (2009) Same host-plant, different sterols: variation in sterol metabolism in an insect herbivore community. J Chem Ecol 35:1309–1319

Janson EM, Peeden ER, Stireman JO III, Abbot P (2010) Symbiont-mediated phenotypic variation without co-evolution in an insect–fungus association. J Evol Biol 23:2212–2228

Jenkins RL, Loxdale HD, Brookes CP, Dixon AFG (1999) The major carotenoid pigments of the grain aphid, *Sitobion avenae* (F.) (Hemiptera: Aphididae). Physiol Entomol 24:171–178

Jurkiewicz BA, Buettner GR (1994) Ultraviolet light induced free-radical formation in skin—an electron paramagnetic resonance study. Photochem Photobiol 59:1–4

Kaissling KE (1996) Peripheral mechanisms of pheromone reception in moths. Chem Senses 21:257–268

Kayser H (1982) Carotenoids in insects. In: Britton G, Goodwin TW (eds) Carotenoid chemistry and biochemistry: proceedings of the 6th international symposium on carotenoids. Pergamon Press, New York, pp 195–210

Kende H, Zeevaart JAD (1997) The five ''classical'' plant hormones. Plant Cell 9:1197–1210

Kettner J, Dorffling K (1995) Biosynthesis and metabolism of abscisic acid in tomato leaves infected with *Botrytis cinerea*. Planta 196:627–634

Kiefer C, Sumser E, Wernet MF, von Lintig J (2002) A class B scavenger receptor mediates the cellular uptake of carotenoids in *Drosophila*. Proc Natl Acad Sci USA 99:10581–10586

Kodric-Brown A, Brown JH (1984) Truth in advertising—the kinds of traits favored by sexual selection. Am Nat 124:309–323

Koga H, Dohi K, Mori M (2004) Abscisic acid and low temperatures suppress the whole plant-specific resistance reaction of rice plants to the infection of *Magnaporthe grisea*. Physiol Mol Plant Pathol 65:3–9

Kunkel BN, Brooks DM (2002) Cross talk between signaling pathways in pathogen defense. Curr Opin Plant Biol 5:325–331

Langley SA, Tilmon KJ, Cardinale BJ, Ives AR (2006) Learning by the parasitoid wasp, *Aphidius ervi* (Hymenoptera: Braconidae), alters individual fixed preferences for pea aphid color morphs. Oecologia 150:172–179

Lev-Yadun S, Gould KS (2007) What do red and yellow autumn leaves signal? Bot Rev 73:279–289

Lewinsohn E, Sitrit Y, Bar E, Azulay Y, Ibdah M, Meir A, Yosef E, Zamir D, Tadmor Y (2005a) Not just colors—carotenoid degradation as a link between pigmentation and aroma in tomato and watermelon fruit. Trends Food Sci Technol 16:407–415

Lewinsohn E, Sitrit Y, Bar E, Azulay Y, Meir A, Zamir D, Tadmor Y (2005b) Carotenoid pigmentation affects the volatile composition of tomato and watermelon fruits, as revealed by comparative genetic analyses. J Agric Food Chem 53:3142–3148

Lichtenthaler HK (1999) The 1-deoxy-D-xylulose-5-phosphate pathway of isoprenoid biosynthesis in plants. Annu Rev Plant Physiol Plant Mol Biol 50:47–65

Lopez-Raez JA, Charnikhova T, Gomez-Roldan V, Matusova R, Kohlen W, De Vos R, Verstappen F, Puech-Pages V, Becard G, Mulder P, Bouwmeester H (2008) Tomato strigolactones are derived from carotenoids and their biosynthesis is promoted by phosphate starvation. New Phytol 178:863–874

Lorenzo O, Solano R (2005) Molecular players regulating the jasmonate signalling network. Curr Opin Plant Biol 8:532–540

Losey JE, Ives AR, Harmon J, Ballantyne F, Brown C (1997) A polymorphism maintained by opposite patterns of parasitism and predation. Nature 388:269–272

Ma ZH, Morgan DP, Michailides TJ (2001) Effects of water stress on *Botryosphaeria* blight of pistachio caused by *Botryosphaeria dothidea*. Plant Dis 85:745–749

Maffei M, Bossi S, Spiteller D, Mithofer A, Boland W (2004) Effects of feeding *Spodoptera littoralis* on lima bean leaves. I. Membrane potentials, intracellular calcium variations, oral secretions, and regurgitate components. Plant Physiol 134:1752–1762

Maleck K, Dietrich RA (1999) Defense on multiple fronts: how do plants cope with diverse enemies? Trends Plant Sci 4:215–219

Matusova R, Rani K, Verstappen FWA, Franssen MCR, Beale MH, Bouwmeester HJ (2005) The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanche* spp. are derived from the carotenoid pathway. Plant Physiol 139:920–934

Mauch-Mani B, Mauch F (2005) The role of abscisic acid in plant-pathogen interactions. Curr Opin Plant Biol 8:409–414

Mayek-Perez N, Garcia-Espinosa R, Lopez-Castaneda C, Acosta-Gallegos JA, Simpson J (2002) Water relations, histopathology and growth of common bean (*Phaseolus vulgaris* L.) during pathogenesis of *Macrophomina phaseolina* under drought stress. Physiol Mol Plant Pathol 60:185–195

McAuslane HJ, Chen J, Carle RB, Schmalstig J (2004) Influence of *Bemisia argentifolii* (Homoptera: Aleyrodidae) infestation and squash silverleaf disorder on zucchini seedling growth. J Econ Entomol 97:1096–1105

McDonald KL, Cahill DM (1999) Influence of abscisic acid and the abscisic acid biosynthesis inhibitor, norflurazon, on interactions between *Phytophthora sojae* and soybean (*Glycine max*). Eur J Plant Pathol 105:651–658

Mehdy MC (1994) Active oxygen species in plant defense against pathogens. Plant Physiol 105:467–472

Meinwald J, Erickson K, Hartshor M, Meinwald YC, Eisner T (1968) Defensive mechanisms of arthropods. 23. An allenic sesquiterpenoid from grasshopper *Romalea microptera*. Tetrahedron Lett 9:2959–2962

Mikheyev AS, Mueller UG, Abbot P (2006) Cryptic sex and many-to-one coevolution in the fungus-growing ant symbiosis. Proc Natl Acad Sci USA 103:10702–10706

Moczek A, Nijhout H (2002) Developmental mechanisms of threshold evolution in a polyphenic beetle. Evol Dev 4:252–264

Mohr PG, Cahill DM (2003) Abscisic acid influences the susceptibility of *Arabidopsis thaliana* to *Pseudomonas syringae* pv. *tomato* and *Peronospora parasitica*. Funct Plant Biol 30:461–469

Mohr PG, Cahill DM (2007) Suppression by ABA of salicylic acid and lignin accumulation and the expression of multiple genes, in *Arabidopsis* infected with *Pseudomonas syringae* pv. *tomato*. Funct Integr Genomics 7:181–191

Moran NA (2002) The ubiquitous and varied role of infection in the lives of animals and plants. Am Nat 160:S1–S8

Moran NA, Jarvik T (2010) Lateral transfer of genes from fungi underlies carotenoid production in aphids. Science 328:624–627

Mothes U, Seitz KA (1982) Fine structural alterations of bean plant leaves by feeding injury of *Tetranychus urticae* Koch (Acari, Tetranychidae). Acarologia 23:149–157

Ni XZ, Quisenberry SS, Heng-Moss T, Markwell J, Higley L, Baxendale F, Sarath G, Klucas R (2002) Dynamic change in photosynthetic pigments and chlorophyll degradation elicited by cereal aphid feeding. Entomol Exp Appl 105:43–53

Nijhout HF (1991) The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington, DC

Nishida R, Rothschild M, Mummery R (1994) Cyanoglucoside, sarmentosin, from the magpie moth, *Abraxas grossulariata*, Geometridae, Lepidoptera. Phytochemistry 36:37–38

Noor MAF, Parnell RS, Grant BS (2008) A reversible color polyphenism in American peppered moth (*Biston betularia cognataria*) caterpillars. PLoS ONE. doi:10.1371/journal.pone.0003142

Norman SM, Maier VP, Pon DL (1990) Abscisic acid accumulation and carotenoid and chlorophyll content in relation to water stress and leaf age of different types of citrus. J Agric Food Chem 38:1326–1334

Oberhauser KS, Cansler D, Feitl A (1996) Genetics of a "zebra" pigment mutation in the larvae of *Danaus plexippus*, L. (Nymphalidae: Danainae). J Lepid Soc 50:237–244

Ohmiya A, Kishimoto S, Aida R, Yoshioka S, Sumitomo K (2006) Carotenoid cleavage dioxygenase (CmCCD4a) contributes to white color formation in chrysanthemum petals. Plant Physiol 142:1193–1201

Ojala K, Julkunen-Tiito R, Lindstrom L, Mappes J (2005) Diet affects the immune defence and life-history traits of an Arctiid moth *Parasemia plantaginis*. Evol Ecol Res 7:1153–1170

Oliveira DC, Isaias RMS, Moreira ASFP, Magalhaes TA, Lemos-Filho JP (2011) Is the oxidative stress caused by *Aspidosperma* spp. galls capable of altering leaf photosynthesis? Plant Sci 180:489–495

Owen CR, Bradshaw HD (2011) Induced mutations affecting pollinator choice in *Mimulus lewisii* (Phrymaceae). Arthropod Plant Interact 5:235–244

Pfander H (1992) Carotenoids—an overview. Meth Enzymol 213: 3–13

Pichersky E (2008) Raging hormones in plants. Nat Chem Biol 4:584–586

Poff JM (1976) Carotenoids of some aposematic and cryptic *Leptinotarsa* (Coleoptera: Chrysomelidae). Am Zool 16:271

Pogson B, McDonald KA, Truong M, Britton G, DellaPenna D (1996) Arabidopsis carotenoid mutants demonstrate that lutein is not essential for photosynthesis in higher plants. Plant Cell 8:1627–1639

Ramel F, Birtic S, Ginies C, Soubigou-Taconnat L, Triantaphylides C, Havaux M (2012) Carotenoid oxidation products are stress signals that mediate gene responses to singlet oxygen in plants. Proc Natl Acad Sci U S A 109:5535–5540

Rey LA (1992) Developmental morphology of two types of hymenopterous galls. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 87–101

Rhainds M, Doyon J, Rivoal J, Brodeur J (2007) Thrips-induced damage of chrysanthemum inflorescences: evidence for enhanced leakage of carotenoid pigments. Entomol Exp Appl 123:247–252

Ritland DB, Brower LP (1991) The viceroy butterfly is not a batesian mimic. Nature 350:497–498

Rothschild M (1991) Is the viceroy a batesian mimic? Nature 351:611–612

Rothschild M, Mummery R (1985) Carotenoids and bile pigments in danaid and swallowtail butterflies. Biol J Linn Soc 24:1–14

Rothschild M, Gardiner B, Mummery R (1978) Role of carotenoids in “golden glance” of danaid pupae (Insecta: Lepidoptera). J Zool 186:351–358

Rothschild M, Mummery R, Farrell C (1986) Carotenoids of butterfly models and their mimics (Lep, Papilionidae and Nymphalidae). Biol J Linn Soc 28:359–372

Sakudoh T, Sezutsu H, Nakashima T, Kobayashi I, Fujimoto H, Uchino K, Banno Y, Iwano H, Maekawa H, Tamura T, Kataoka H, Tsuchida K (2007) Carotenoid silk coloration is controlled by a carotenoid-binding protein, a product of the yellow blood gene. Proc Natl Acad Sci USA 104:8941–8946

Salt SD, Tuzun S, Kuc J (1986) Effects of beta-ionone and abscisic acid on the growth of tobacco and resistance to blue mold. Mimicry of effects of stem infection by *Peronospora tabacina* Adam. Physiol Mol Plant Pathol 28:287–297

Sandre S, Tammaru T, Esperk T, Julkunen-Tiitto R, Mappes J (2007) Carotenoid-based colour polyphenism in a moth species: search for fitness correlates. Entomol Exp Appl 124:269–277

Schaefer HM, Rolshausen G (2006) Plants on red alert: do insects pay attention? BioEssays 28:65–71

Scherzinger D, Al-Babili S (2008) In vitro characterization of a carotenoid cleavage dioxygenase from *Nostoc* sp. PCC 7120 reveals a novel cleavage pattern, cytosolic localization and induction by highlight. Mol Microbiol 69:231–244

Schiestl FP, Steinebrunner F, Schulz C, von Reuss S, Francke W, Weymuth C, Leuchtmann A (2006) Evolution of ‘pollinator’—attracting signals in fungi. Biol Lett (London, U K) 2:401–404

Schimek C, Wöstemeyer J (2006) Pheromone action in the fungal groups Chytridiomycota, and Zygomycota, and in the Oomycota. In: Kues U, Fischer R (eds) The Mycota: volume I: growth, differentiation, and sexuality, 2nd edn. Springer-Verlag, New York, pp 215–231

Schmidt K, Pflugmacher M, Klages S, Maeser A, Mock A, Stahl DJ (2008) Accumulation of the hormone abscisic acid (ABA) at the infection site of the fungus *Cercospora beticola* supports the role of ABA as a repressor of plant defence in sugar beet. Mol Plant Pathol 9:661–673

Scholes JD, Press MC (2008) Striga infestation of cereal crops—an unsolved problem in resource limited agriculture. Curr Opin Plant Biol 11:180–186

Schulz S, Boppre M, Vanewright RI (1993) Specific mixtures of secretions from male scent organs of African milkweed butterflies (Danainae). Philos Trans R Soc B 342:161–181

Schuster DJ, Mueller TF, Kring JB, Price JF (1990) Relationship of the sweet-potato whitefly to a new tomato fruit disorder in Florida. HortScience 25:1618–1620

Schwartz SH, Zeevaart JAD (2004) Abscisic acid biosynthesis and metabolism. In: Davies PJ (ed) Plant hormones biosynthesis, signal transduction, action!, 3rd edn. Kluwer Academic Publishers, Boston, pp 137–155

Shao Y, Spiteller D, Tang X, Ping L, Colesie C, Muenchberg U, Bartram S, Schneider B, Buedel B, Popp J, Heckel DG, Boland W (2011) Crystallization of alpha- and beta-carotene in the foregut of *Spodoptera* larvae feeding on a toxic food plant. Insect Biochem Mol Biol 41:273–281

Shawkey MD, Morehouse NI, Vukusic P (2009) A protean palette: colour materials and mixing in birds and butterflies. J R Soc Interface 6:S221–S231

Shindo Y, Witt E, Han D, Packer L (1994) Dose-response effects of acute ultraviolet-irradiation on antioxidants and molecular markers of oxidation in murine epidermis and dermis. J Invest Dermatol 102:470–475

Shukolyukov SA, Saakov VS (2001) American cockroach (*Periplaneta americana*) synthesizes carotenoids from the precursor [C-14] mevalonic acid pyrophosphate. Biochemistry (Moscow) 66:535–540

Simkin AJ, Schwartz SH, Auldridge M, Taylor MG, Klee HJ (2004) The tomato carotenoid cleavage dioxygenase 1 genes contribute to the formation of the flavor volatiles beta-ionone, pseudoionone, and geranylacetone. Plant J 40:882–892

Smilanich AM, Mason PA, Sprung L, Chase TR, Singer MS (2011) Complex effects of parasitoids on pharmacophagy and diet choice of a polyphagous caterpillar. Oecologia 165:995–1005

Sommerburg O, Langhans CD, Arnhold J, Leichsenring M, Salerno C, Crifo C, Hoffmann GF, Debatin KM, Siems WG (2003) Beta-carotene cleavage products after oxidation mediated by hypochlorous acid—a model for neutrophil-derived degradation. Free Radical Biol Med 35:1480–1490

Spoel SH, Koornneef A, Claessens SMC, Korzelius JP, Van Pelt JA, Mueller MJ, Buchala AJ, Metraux JP, Brown R, Kazan K, Van Loon LC, Dong XN, Pieterse CMJ (2003) NPR1 modulates cross-talk between salicylate- and jasmonate-dependent defense pathways through a novel function in the cytosol. Plant Cell 15:760–770

Starnecker G (1997) Hormonal control of lutein incorporation into pupal cuticle of the butterfly *Inachis io* and the pupal melanization reducing factor. Physiol Entomol 22:65–72

Stavenga DG (2006) Invertebrate photoreceptor optics. In: Warrant E, Nilsson DE (eds) Invertebrate vision. Cambridge University Press, New York, pp 1–42

Steinkellner S, Lendzemo V, Langer I, Schweiger P, Khaosaad T, Toussaint JP, Vierheilig H (2007) Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant-fungus interactions. Molecules 12:1290–1306

Stevens MA (1970) Relationship between polyene carotene content and volatile compound composition of tomatoes. J Am Soc Hort Sci 95:461–464

Stireman JO III, Janson EM, Carr TG, Devlin H, Abbot P (2008) Evolutionary radiation of *Asteromyia carbonifera* (Diptera: Cecidomyiidae) gall morphotypes on the goldenrod *Solidago altissima* (Asteraceae). Biol J Linn Soc 95:840–858

Stireman JO III, Devlin H, Carr TG, Abbot P (2010) Evolutionary diversification of the gall midge genus *Asteromyia* (Cecidomyiidae) in a multitrophic ecological context. Mol Phylogenet Evol 54:194–210

Stratton SP, Schaefer WH, Liebler DC (1993) Isolation and identification of singlet oxygen oxidation-products of beta-carotene. Chem Res Toxicol 6:542–547

Suzuki S, Nishihara M, Nakatsuka T, Misawa N, Ogiwara I, Yamamura S (2007) Flower color alteration in *Lotus japonicus* by modification of the carotenoid biosynthetic pathway. Plant Cell Rep 26:951–959

Suzuki T, Watanabe M, Takeda M (2009) UV tolerance in the two-spotted spider mite, *Tetranychus urticae*. J Insect Physiol 55:649–654

Telfer A, Pascal A, Gall A (2008) Carotenoids in photosynthesis. In: Britton G, Liaane-Jensen S, Pfander H (eds) Carotenoids volume 4: natural functions. Birkhäuser Verlag, Boston, pp 265–308

Tewksbury JJ, Nabhan GP (2001) Seed dispersal—directed deterrence by capsaicin in chillies. Nature 412:403–404

Tewksbury JJ, Reagan KM, Machnicki NJ, Carlo TA, Haak DC, Penaloza ALC, Levey DJ (2008) Evolutionary ecology of pungency in wild chilies. Proc Natl Acad Sci USA 105: 11808–11811

Thaler JS, Bostock RM (2004) Interactions between abscisic-acid-mediated responses and plant resistance to pathogens and insects. Ecology 85:48–58

Tooker JF, De Moraes CM (2007) Feeding by Hessian fly [*Mayetiola destructor* (Say)] larvae does not induce plant indirect defences. Ecol Entomol 32:153–161

Tooker JF, De Moraes CM (2008) Gall insects and indirect plant defenses: a case of active manipulation? Plant Signal Behav 3:503–504

Tooker JF, Rohr JR, Abrahamson WG, De Moraes CM (2008) Gall insects can avoid and alter indirect plant defenses. New Phytol 178:657–671

Umehara M, Hanada A, Yoshida S, Akiyama K, Arite T, Takeda-Kamiya N, Magome H, Kamiya Y, Shirasu K, Yoneyama K, Kyozuka J, Yamaguchi S (2008) Inhibition of shoot branching by new terpenoid plant hormones. Nature 455:195–200

Van der Veen IT (2005) Costly carotenoids: a trade-off between predation and infection risk? J Evol Biol 18:992–999

Vasyuk VA, Andrianova TV, Musatenko LI (1996) Abscisic acid of phytopathogenic fungi *Septoria tritici* Rob. ex Desm. and *Stagonospora nodorum* (Berk.) Cast. et Germ. Ukrayins'kyi Botanichnyi Zhurnal 53:58–62

Veerman A (2001) Photoperiodic time measurement in insects and mites: a critical evaluation of the oscillator-clock hypothesis. J Insect Physiol 47:1097–1109

Veerman A, Veenendaal RL (2003) Experimental evidence for a non-clock role of the circadian system in spider mite photoperiodism. J Insect Physiol 49:727–732

Vizarova G, Chalanyova M, Janitor A, Dugova O, Bacigalova K, Takac L (1997) Secretion of abscisic acid by hemibiotrophic fungi. Biologia 52:807–809

Vogel JT, Tan BC, McCarty DR, Klee HJ (2008) The carotenoid cleavage dioxygenase 1 enzyme has broad substrate specificity, cleaving multiple carotenoids at two different bond positions. J Biol Chem 283:11364–11373

von Lintig J, Dreher A, Kiefer C, Wernet MF, Vogt K (2001) Analysis of the blind *Drosophila* mutant ninaB identifies the gene encoding the key enzyme for vitamin A formation in vivo. Proc Natl Acad Sci USA 98:1130–1135

Walter MH, Strack D (2011) Carotenoids and their cleavage products: biosynthesis and functions. Nat Prod Rep 28:663–692

Ward EWB, Cahill DM, Bhattacharyya MK (1989) Abscisic acid suppression of phenylalanine ammonia-lyase activity and mRNA, and resistance of soybeans to *Phytophthora megasperma* f.sp. *glycinea*. Plant Physiol 91:23–27

Wasilewska A, Vlad F, Sirichandra C, Redko Y, Jammes F, Valon C, Frey NFD, Leung J (2008) An update on abscisic acid signaling in plants and more. Mol Plant 1:198–217

Wei S, Hannoufa A, Soroka J, Xu N, Li X, Zebarjadi A, Gruber M (2011) Enhanced beta-ionone emission in *Arabidopsis* over-expressing AtCCD1 reduces feeding damage in vivo by the crucifer flea beetle. Environ Entomol 40:1622–1630

Weisgraber KH, Lousberg RJ, Weiss U (1971) Chemical basis of color dimorphism of an aphid, *Macrosiphum liriodendri* (Monell), and a locust, *Amblycorypha* sp. novel carotenoids. Experientia 27:1017–1018

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, New York

Westphal E (1992) Cecidogenesis and resistance phenomena in mite-induced galls. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford University Press, New York, pp 141–156

White TCR (2010) Why do many galls have conspicuous colours? An alternative hypothesis revisited. Arthropod Plant Interact 4: 149–150

Whitney HM, Glover BJ (2007) Morphology and development of floral features recognised by pollinators. Arthropod Plant Interact 1:147–158

Whitney KD, Stanton ML (2004) Insect seed predators as novel agents of selection on fruit color. Ecology 85:2153–2160

Wilkinson DM, Sherratt TN, Phillip DM, Wratten SD, Dixon AFG, Young AJ (2002) The adaptive significance of autumn leaf colours. Oikos 99:402–407

Williams RN, Fickle DS, McGovern TP, Klein MG (2000) Development of an attractant for the scarab pest *Macrodactylus subspinosus* (Coleoptera: Scarabaeidae). J Econ Entomol 93: 1480–1484

Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 57:781–803

Yoneyama K, Xie XN, Kusumoto D, Sekimoto H, Sugimoto Y, Takeuchi Y, Yoneyama K (2007a) Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. Planta 227: 125–132

Yoneyama K, Yoneyama K, Takeuchi Y, Sekimoto H (2007b) Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. Planta 225:1031–1038

Zahavi A (1975) Mate selection—selection for a handicap. J Theor Biol 53:205–214

Zervoudakis G, Tairis N, Salahas G, Georgiou CD (2003) Beta-carotene production and sclerotial differentiation in *Sclerotinia minor*. Mycol Res 107:624–631

Zheng SJ, Snoeren TAL, Hogewoning SW, van Loon JJA, Dicke M (2010) Disruption of plant carotenoid biosynthesis through virus-induced gene silencing affects oviposition behaviour of the butterfly *Pieris rapae*. New Phytol 186:733–745

Zorn H, Langhoff S, Scheibner M, Nimtz M, Berger RG (2003) A peroxidase from Lepista irina cleaves ß, ß-carotene to flavor compounds. Biol Chem 384:1049–1056