

Chapter 4

Leaf Trichome Formation and Plant Resistance to Herbivory

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Leaf trichomes contribute to plant resistance against herbivory. In several plant species, the trichome density of new leaves increases after herbivore damage. Here we review the genetic basis of trichome production and the functional and adaptive significance of constitutive and induced trichome formation. We focus on leaf trichomes and their production in response to damage caused by herbivores. The genetic basis of trichome production has been explored in detail in the model species *Arabidopsis thaliana*. Recent comparative work indicates that the regulatory networks governing trichome development vary and that trichome production has evolved repeatedly among angiosperms. Induced trichome production has been related to increased levels of jasmonic acid in *Arabidopsis*, indicating a common link to other changes in resistance characteristics. Damage from insect herbivores is oftentimes negatively related to trichome production, and enhanced trichome production may thus be advantageous as it increases resistance against herbivores. There are yet few studies exploring the costs and benefits of induced trichome production in terms of plant fitness. Trichome density affects interactions with insect herbivores, but may also affect the abundance and effectiveness of predators and parasitoids feeding on herbivores, and the tolerance to abiotic stress. This suggests that an improved understanding of the functional and adaptive significance of induced trichome production requires field studies that consider the effects of trichome density on antagonistic interactions, tritrophic interactions, and plant fitness under contrasting abiotic conditions.

4.1 Introduction

Trichomes are hair-like appendages that develop from cells of the aerial epidermis and are produced by most plant species (Werker 2000). Leaf trichomes can serve several functions including protection against damage from herbivores (Levin 1973).

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While most plants produce trichomes constitutively, some species respond to damage by increasing trichome density in new leaves. The purpose of this paper is to review processes affecting trichome formation, and the importance of trichomes in plant resistance. We mainly focus on leaf trichomes and their production in response to damage caused by herbivorous insects. We begin by briefly reviewing current understanding of the genetic basis of trichome formation. Based on literature data, we explore the magnitude of damage-induced increases in trichome production and the hormonal basis of damage-induced trichome production. We then discuss the effects of induced trichome production on interactions with herbivorous insects, their natural enemies and on plant fitness. Finally, we identify problems in need of further research for a better understanding of the functional and adaptive significance of induced trichome production in plants.

The morphology and density of leaf trichomes vary considerably among plant species, and may also vary among populations and within individual plants. The structure of trichomes can range from unicellular to multi-cellular, and the trichomes can be straight, spiral, hooked, branched, or un-branched (Southwood 1986; Werker 2000). Some trichomes have glands that release secondary metabolites (e.g., terpenes and alkaloids) which can be poisonous, repellent, or trap insects and other organisms. These trichomes are commonly referred to as glandular trichomes (Duffey 1986). In some species, individual plants produce both glandular and non-glandular leaf trichomes (e.g., Hare and Elle 2002; Rautio et al. 2002).

Trichome production is an important component of resistance against herbivorous insects (Levin 1973; Southwood 1986; Ågren and Schemske 1994; Karban and Baldwin 1997; Traw and Dawson 2002a). Damage from many insect herbivores is negatively related to trichome density (Ågren and Schemske 1993; Mauricio 1998; Valverde et al. 2001; Hare and Elle 2002; Handley et al. 2005). The glabrous (non-hairy) morph of the perennial herb *Arabidopsis lyrata* is more damaged by insect herbivores than the trichome-producing morph (Løe et al. 2007), and experimental removal of leaf trichomes resulted in increased feeding and growth of herbivorous insects in bioassay studies of several species (Rowell-Rahier and Pasteels 1982; Baur et al. 1991; Fordyce and Agrawal 2001). Moreover, several plant species respond to damage caused by herbivores by producing new leaves with an increased density and/or number of trichomes (Table 4.1), and insects feeding on the induced plants often consume less foliage and grow less well compared with insects on non-induced plants (Agrawal 1999; 2000; Dalin and Björkman 2003). These studies indicate that the production of leaf trichomes contributes to the protection against herbivorous insects.

Leaf trichomes may also increase resistance to abiotic stress. They may increase tolerance to drought by reducing absorbance of solar radiation and increasing the leaf surface boundary layer (Ehrlinger 1984; Choinski and Wise 1999; Benz and Martin 2006), and by facilitating condensation of air moisture onto the plant surface (Jeffree 1986). Trichomes may further protect living cells from damage caused by solar UV-radiation (Skaltsa et al. 1994), and low temperatures (Agrawal et al. 2004). Trichomes may thus have multiple functions and trichome density may evolve in response to variation in several environmental factors. In general, plants with high

Table 4.1 Induced increases in trichome density recorded after artificial wounding and damage by insect herbivores

Plant Species (life history) ¹	Defoliation treatment		Increase in trichome density		Reference	
	Damage	Environment	Amount	Tissue damaged		
<i>Arabidopsis thaliana</i> (a)	Artificial	Lab	Pinching	Leaves	25%–117% weeks	Traw and Bergelson (2003)
<i>Alnus incana</i> (p)	Coleoptera	Field	30%–100%	Leaves	500%	Baur et al. (1991)
<i>Brassica nigra</i> (a)	Lepidoptera	Lab	25%	Leaves	76% weeks	Traw and Dawson (2002a)
<i>Brassica nigra</i> (a)	Lepidoptera	Lab	25%	Leaves	113% weeks	Traw and Dawson (2002a)
<i>Brassica nigra</i> (a)	Coleoptera	Lab	17%	Leaves	no induction weeks	Traw and Dawson (2002a)
<i>Brassica nigra</i> (a)	Lepidoptera	Lab	25%	Leaves	43%	Dawson (2002a)
<i>Brassica nigra</i> (a)	Coleoptera	Lab	25%	Leaves	no induction weeks	Traw and Dawson (2002b)
<i>Brassica nigra</i> (a)	Lepidoptera	Lab	22%	Leaves	38%	Dawson (2002b)
<i>Betula pubescens</i> (p)	Artificial	Field	50%	Leaves	2%–3 weeks	Traw 2002
<i>Betula pubescens</i> (p)	Artificial	Field	100%	Leaves	2%–7 weeks (1998)	Rautio et al. (2002)
<i>Betula pubescens</i> (p)	Artificial	Field	50%	Leaves	2%–7 weeks (1998)	Rautio et al. (2002)
<i>Betula pubescens</i> (p)	Artificial	Field	100%	Leaves	no induction weeks	Rautio et al. (2002)
<i>Betula pubescens</i> (p)	Artificial	Field	100%	Leaves	no induction weeks	Rautio et al. (2002)
<i>Betula pubescens</i> (p)	Artificial	Field	≤ 25%	Leaves	10%–20% next year	Valkama et al. (2005)
<i>Betula pubescens</i> (p)	Artificial	Field	10 cm	Shoots	no induction next year	Valkama et al. (2005)

Table 4.1 (continued)

	Defoliation treatment			Increase in trichome density		Reference	
	Damage	Environment	Amount	Tissue damaged	Magnitude		Timing
<i>Cnidocolus texanus</i> (p)	Livestock	Field	no info.	Shoots	38%	no info.	Pollard (1986)
<i>Lepidium virginicum</i> (a)	Lepidoptera	Lab	20%–25%	Leaves	60%	2 weeks	Agrawal (2000)
<i>Raphanus raphanistrum</i> (a)	Lepidoptera	Lab	50%	Leaves	25%–100%	3 weeks	Agrawal (1999)
<i>Salix borealis</i> (p)	Coleoptera	Field	100%	Leaves	51%–300%	next year	Zvereva et al. (1998)
<i>Salix cinerea</i> (p)	Coleoptera	Lab	5%	Leaves	72%	3 weeks	Dalin and Björkman (2003)
<i>Salix cinerea</i> (p)	Artificial	Lab	5%	Leaves	no induction	3 weeks	Dalin and Björkman (2003)
<i>Salix cinerea</i> (p)	Coleoptera	Lab	10%	Leaves	93%	3 weeks	Björkman and Ahne (2005)
<i>Salix cinerea</i> (p)	Coleoptera	Lab	3%	Leaves	83%–186%	3 weeks	Björkman et al. (2008)
<i>Salix viminalis</i> (p)	Coleoptera	Lab	5%–25%	Leaves	13%	3 weeks	Dalin et al. (2004)
<i>Urtica dioica</i> (p)	Artificial	Field	>50%	Shoots	140%–790%	10 weeks	Pullin and Gilbert (1989)
<i>Urtica dioica</i> (p)	Artificial	Lab	>50%	Shoots	23%–106%	10 weeks	Pullin and Gilbert 1989
<i>Urtica dioica dioica</i> (p)	Artificial	Lab	50%	Leaves	26%	5–7 weeks	Mutikainen and Walls (1995)
<i>Urtica dioica dioica</i> (p)	Artificial	Lab	No info.	Apical buds	no induction	5–7 weeks	Mutikainen and Walls (1995)
<i>Urtica dioica sondenii</i> (p)	Artificial	Lab	50%	Leaves	no induction	5–7 weeks	Mutikainen and Walls (1995)
<i>Urtica dioica sondenii</i> (p)	Artificial	Lab	No info.	Apical buds	50%	5–7 weeks	Mutikainen and Walls (1995)

¹The life history of the different plant species is indicated as (p) for perennial, or (a) for annual

density of leaf trichomes can be expected in environments that are dry or cold, where UV-radiation is intense, and in areas where the risk of being damaged by herbivorous insects is high (Ehrlinger 1984; Løe et al. 2007).

4.2 Leaf Trichome Formation

4.2.1 Molecular Basis of Leaf Trichome Formation

Trichomes are initiated in the epidermis of developing leaves: some epidermal cells will develop into trichome cells whereas surrounding cells will develop into regular epidermal cells. Present understanding of trichome formation is based on studies of a few model species. In particular, trichome formation in *A. thaliana* has been used as a model system to study various developmental and cellular mechanisms in plants. In *Arabidopsis*, trichomes are non-glandular, large single cells, surrounded by accessory epidermal cells on rosette leaves, stems, cauline leaves, and sepals. With mutagenesis screens, dozens of genes involved in trichome initiation, spacing, and shape have been identified in *Arabidopsis* (Marks 1997; Hülskamp and Schnittger 1998). Recent studies of *A. thaliana* and its close relatives have shown that variation in some of the same genes can explain differences in trichome formation in natural populations (Hauser et al. 2001; Kivimäki et al. 2007).

Studies of the genetic basis of trichome initiation have identified genes that (a) control the entry into the trichome pathway and (b) control the spacing of initiation events. Loss-of-function mutations in *A. thaliana* have suggested that the genes *GLABROUS1* (*GL1*) and *TRANSPARENT TESTA GLABRA1* (*TTG1*) are important for both the initiation and spacing of leaf trichomes. *GL1* encodes a myb-transcription factor that is expressed diffusively in developing leaves (Oppenheimer et al. 1991). *TTG1* is expressed in most major plant organs, codes for a WD-40 repeat-containing protein, and is needed for trichome cell initiation in leaves, non-hair cell type (atrachoblast) formation in roots, anthocyanin biosynthesis in leaves, and formation of mucilage layer in germinating seeds (Koornneef 1981; Walker et al. 1999). For normal trichome initiation, the genes *GLABROUS3* (*GL3*) and *ENHANCER OF GLABRA3* (*EGL3*), which code for helix-loop-helix (bHLH) proteins, are also needed (Payne et al. 2000; Zhang et al. 2003). *GL1* and *TTG1* have the capacity to limit trichome initiation together with other genes, e.g., *CAPRICE* (*CPC*) and *TRIPTYCHON* (*TRY*) that are known to promote root hair cell fate (Szymanski et al. 2000; Schiefelbein 2003). The gene *GLABROUS2* (*GL2*) quantitatively regulates the frequency of trichome initiation and is involved in determining trichome spacing and root hair development (Ohashi and Oka 2002), but is also involved in the control of seed oil accumulation (Shen et al. 2006). Thus, many genes involved in trichome initiation and spacing also regulate other important phenotypic traits, which may constrain the evolution of genes and traits.

Although current understanding of the genetic basis of trichome initiation and spacing depends to a large degree on studies of mutants in *Arabidopsis*, some

information is also available for other plant species. Trichome initiation in cotton seems to be regulated by a similar multimeric complex between MYB, bHLH and WD repeat proteins as in *Arabidopsis* (Wang et al. 2004). Sequence comparisons and functional analyses suggest that genes underlying trichome formation in *Arabidopsis* (and perhaps cotton) may have evolved from duplication and neo-functionalization of genes involved in anthocyanin and flavonoid production, whereas the genes involved in the formation of analogous multicellular trichomes in *Nicotiana* and *Antirrhinum* have a different origin (Serna and Martin 2006). Thus, trichome production appears to have evolved several times suggesting convergent adaptive evolution.

4.2.2 Genetic Basis of Natural Variation in Trichome Production

Both trichome production as such (trichome production vs. glabrousness) and the type of trichomes produced (glandular vs. non-glandular) may vary within species. Many plant species are polymorphic for trichome production with trichome-producing and glabrous morphs. In several species, the frequency of the trichome-producing morph varies geographically, among and within habitats (Björkman and Anderson 1990; Westerberg and Saura 1992; Barnes and Han 1993; St Hilaire and Graves 1999; Arroyo-García et al. 2001; Morrison 2002; Kärkkäinen et al. 2004; Løe et al. 2007). Genetic analyses have shown that the inheritance of the glabrous morph is simple in many species (one gene with a recessive allele for glabrousness; e.g., Westerbergh and Saura 1992; Sharma and Waines 1994; Kärkkäinen and Ågren 2002). In *A. lyrata*, association analysis of phenotypic variation and genotypic variation in candidate genes revealed that the polymorphism in trichome production was caused by variation in *GLABROUS1* (Kivimäki et al. 2007), and sequence analysis suggested that several independent mutations in the same gene cause glabrousness in different natural populations of *A. lyrata* and *A. thaliana* (Kivimäki et al. 2007; Hauser et al. 2001). Polymorphism in trichome morphology (glandular vs. non-glandular trichomes) can also be inherited in a simple Mendelian fashion, as documented for *Datura wrightii* (van Dam et al. 1999).

The number of trichomes produced and trichome density vary genetically within several species. Quantitative genetic studies have indicated ample genetic variation for trichome number and trichome density (Ågren and Schemske 1994; Mauricio and Rausher 1997; Roy et al. 1999; Clauss et al. 2006). QTL-studies have been conducted to reveal the genetic basis of among-population differences in trichome formation. In *A. thaliana*, a QTL-analysis of a cross between two accessions identified a major QTL for trichome number (*REDUCED TRICHOME NUMBER*, *RTN*) that explained 70% of the variation in number of trichomes produced (Larkin et al. 1996). More recent studies of crosses among other accessions of *A. thaliana* detected additional QTLs (altogether nine QTLs in four different crosses, most of which were shared among populations; Symonds et al. 2005). Preliminary results from QTL-crosses and within-population studies in *A. lyrata* suggest that a limited

number of loci contribute to variation in the number of trichomes produced, and that some genes segregate in several populations also in this species (Kärkkäinen et al. unpublished data).

4.3 Induced Trichome Production

4.3.1 Damage-Induced Trichome Production

Both artificial wounding and damage by herbivores can induce an increase in trichome density, and induction of trichome production has been observed in both annual and perennial plants (Table 4.1). The magnitude of the reported increase in trichome density is typically between 25% and 100%, but in some cases as large as 500%–1000% (Table 4.1). The responses often involve changes in trichome density expressed within days or weeks (Baur et al. 1991; Agrawal 1999, 2000; Rautio et al. 2002; Dalin and Björkman 2003). In some woody perennials, the response is delayed and not observed until the year following initial attack (Zvereva et al. 1998; Valkama et al. 2005). Damage can also induce a change in the relative proportions of glandular and non-glandular trichomes (Rautio et al. 2002).

Abiotic stress, such as drought and UV-radiation, may influence trichome formation (Nagata et al. 1999; Höglund and Larsson 2005), and abiotic conditions may modify damage-induced responses in trichome density. For example, Björkman et al. (2008) showed that the increase in trichome production induced by leaf beetle herbivory in the willow *Salix cinerea* is stronger in the shade than under direct sunlight, suggesting that the plants invested more resources into trichome defense when growing in the shade. The results from Table 4.1 also show that damage-induced increases in trichome density tend to be stronger under field conditions than in the lab. All five studies, in which plants increased the density of leaf trichomes by more than 200% following damage, were conducted in the field. However, empirical data are still few, and additional studies of how abiotic conditions affect damage-induced responses in trichome formation are clearly needed.

Damage has not been observed to induce trichome production in all studies (Table 4.1). Only about half of the 15 independent studies listed in Table 4.1, in which the experimental treatment consisted of artificial wounding (e.g., clipping of leaves) reported an increased trichome density. Also, the effect of damage on trichome production may vary depending on the identity of the herbivore; not all herbivorous insects induce a change in trichome formation (Traw and Dawson 2002a, b). Artificial wounding differs from the damage caused by the feeding of insects in several ways, which may reduce the chances of detecting induced responses (Hartley and Lawton 1987; Cipollini et al. 2003). Moreover, the feeding patterns of insects vary, especially among feeding guilds (e.g., chewers, miners and borers), which may affect how plants respond to damage. Further studies are therefore needed to examine the extent to which responses vary with damage type, and whether plants may benefit from responding differently to different kinds of damage.

4.3.2 Hormonal Regulation of Induced Trichome Production

Recent work on *Arabidopsis* indicates that several regulatory networks may influence damage-induced increases in trichome production. Jasmonic acid regulates the systemic expression of chemical defenses (Karban and Baldwin 1997; Schaller and Stintzi this volume), and herbivore damage as well as artificial wounding cause rapid increases in jasmonic acid (Bostock 1999; Reymond et al. 2000). In *A. thaliana*, artificial damage, but also application of jasmonic acid and application of gibberellin increases trichome production in new leaves (Traw and Bergelson 2003). Application of salicylic acid, on the other hand, reduces trichome production and inhibits the response to jasmonic acid, which is consistent with negative cross-talk between the jasmonate- and salicylate-dependent pathways in *Arabidopsis* (Traw and Bergelson 2003). Concentrations of salicylic acid typically increase in response to infection by biotrophic pathogens (Gaffney et al. 1993; Ryals et al. 1994), but may also increase in response to damage caused by some herbivores (Stotz et al. 2002; van Poecke and Dicke 2002). This suggests that induction of increased trichome production will be affected by interactions with both herbivores and pathogens, and should vary depending on the identity of the herbivore.

4.4 Leaf Trichomes and Plant Resistance

4.4.1 Effects on Herbivore Behavior and Performance

Trichomes influence insect oviposition and/or feeding in a wide range of insects and other herbivores (Levin 1973). Non-glandular trichomes mainly function as a structural defense against small herbivores. They interfere with the movement of insects and other small arthropods over the plant surface and make it more difficult for insects to access the leaf epidermis underneath for feeding (Southwood 1986). Trichomes are often composed of cellulose and other substances that constitute low nutritional value for the insects (Levin 1973). Insects that need to feed through the trichomes before accessing the leaf epidermis might therefore gain less weight and, ultimately, show increased mortality. Glandular trichomes can be viewed as a combination of a structural and chemical defense. This is because the glandular trichomes release secondary metabolites that can be poisonous or repellent to herbivorous organisms. Stinging trichomes, such as those produced by stinging nettles (*Urtica dioica*), may deter even large herbivores (Pollard and Briggs 1984).

The presence and density of leaf trichomes can influence both host-plant selection behavior and performance (i.e., growth, survival, and fecundity) of herbivorous insects, but can be considered a relatively soft ‘weapon’ in plant defense compared with many other traits that are lethal to insects. It has been argued that weak defense traits might influence a wide range of herbivorous insects because they are less likely to result in counter-adaptations in insects (Feeny 1976). For example, there are a number of studies suggesting that leaf trichomes reduce the feeding of both generalist and specialist insects (Traw and Dawson 2002a; Agrawal 1999, 2004). Agrawal (1999) showed that two lepidopteran species, one specialist and

one generalist, were both negatively influenced by previous damage on wild radish plants, which was correlated with an increased density and number of trichomes on the leaves. Agrawal (2004) also showed that several insect feeding guilds, both leaf chewers and leaf miners, were negatively affected by an increased density of leaf trichomes on milkweed (*Asclepias syriaca*). Thus, non-glandular trichomes might influence the feeding by a wide range of insects and therefore reduce total damage caused by herbivores.

Insects may evolve physiological or behavioral traits that allow them to cope with structural plant defenses. For example, several mirid bugs (Heteroptera: Miridae) have special structures on their legs, which facilitate movement across trichome-covered plant surfaces (Southwood 1986; van Dam and Hare 1998). The leaf beetle *Phratora vulgatissima* has been observed to remove non-glandular trichomes when feeding on leaves of the willow *Salix viminalis* (Dalin et al. 2004). This behavior was not observed when the same beetle species was feeding on *S. cinerea*, which produces shorter and broader trichomes that appeared more difficult for the larvae to handle (Dalin and Björkman 2003). The evolution of mouthparts strong enough to handle structural plant traits is thus one possible mechanism for insects to circumvent structural plant defenses such as leaf trichomes (Levin 1973; Raupp 1985).

4.4.2 Effects on Tritrophic Interactions

Leaf trichomes do not only affect herbivores, but also their natural enemies. This may indirectly affect the intensity of damage caused by herbivores. In theory, the effect on the abundance and effectiveness of natural enemies may be neutral (no effect), negative or positive (Fig. 4.1). If we assume that herbivores are affected negatively by leaf trichomes (Fig 4.1; top graph), a neutral effect on the third trophic level will result in natural enemies having an additive effect on plant damage caused by herbivores and on plant fitness. A negative effect on the third trophic level will act antagonistically. Depending on the relative strength of the negative effects of leaf trichomes on herbivores and natural enemies the correlation between trichome density and damage may vary from negative to positive. Plant damage will be (i) negatively correlated with trichome density if the effect on natural enemies is weaker than that on herbivores (dotted line) (ii) uncorrelated with trichome density if the effect on the natural enemies and herbivores balance (solid line), or (iii) positively correlated with trichome density if the effect on natural enemies is stronger than that on the herbivores (dashed line). A positive effect of leaf trichomes on the third trophic level should result in a synergistic positive effect on plant fitness. From a plant protection perspective, this last scenario would be most desirable, but there seem to be few such examples.

In most empirical studies, the abundance and effectiveness of natural enemies were found to be negatively correlated with the density of plant trichomes (Kauffman and Kennedy 1989; Farrar and Kennedy 1991; Nihoul 1993; Gange 1995; Heinz and Zalom 1996; Romeis et al. 1998, 1999; Krips et al. 1999; Rosenheim et al. 1999; Lovinger et al. 2000; Fordyce and Agrawal 2001; Stavrinides and Skirvin 2003; Mulatu et al. 2006; Olson and Andow 2006). The effectiveness of both predators

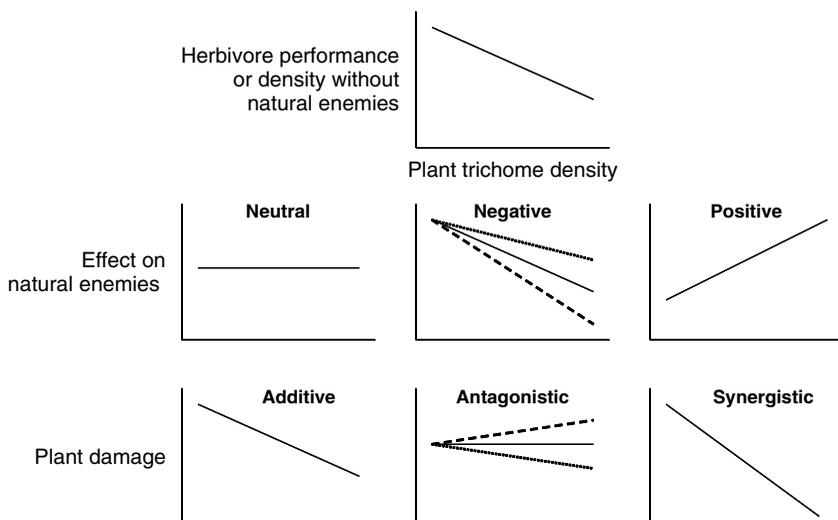


Fig. 4.1 Simplified graphical presentation of how the effect of leaf trichome density on the abundance or effectiveness of predators and parasitoids of herbivores may influence the relationship between trichome density and plant damage caused by herbivores (bottom row of graphs). The natural enemies may not be affected, or may be negatively or positively affected by plant trichome density (middle row of graphs). A basic assumption is that plant trichome density negatively affects herbivore performance or density (top graph), i.e., trichomes have the potential to function as a plant resistance trait (cf. Hare 1992)

(in 9 out of 13 reviewed studies) and parasitoids (in 12 out of 14 reviewed studies) is affected negatively because movement is inhibited and searching time is prolonged. Both non-glandular and glandular plant trichomes can have these effects. Glandular trichomes, in addition, affect natural enemies negatively by (a) the release of repellent or toxic compounds and (b) being sticky and hindering movements. However, the effect of the sticky substances produced by glandular trichomes may sometimes be of little importance in the field as the adhesive effect of the trichome exudates can be negatively affected by dust, wind, and rain (Obrycki and Tauber 1984; Romeis et al. 1999).

In a few cases, the abundance or effectiveness of natural enemies were found to be positively correlated with the density of plant trichomes. For example, Styrsky et al. (2006) recently showed that fire ant predation of herbivores on soybean was higher on isolines of soybean with high trichome density. The suggested mechanism was a functional response by the ants to a higher abundance of caterpillars on pubescent plants. Apple trees producing high density of trichomes had a higher abundance of predatory mites than apple trees with a low density of trichomes, and it has been suggested that this was because pubescent plants capture more pollen and fungal spores that serve as alternative food for the predators (Roda et al. 2003). Lucas and Brodeur (1999) showed that within potato plants, an aphidophagous midge was more abundant on leaves with a high trichome density. The authors

suggested that both a decreased risk of intraguild predation by e.g., coccinelids and a higher density of food (i.e., aphids) on leaves with a high trichome density may have contributed to this pattern. Finally, leaf trichome exudates may serve as extrafloral nectar for a scelonid egg parasitoid of squash bugs (Olson and Nechols 1995). Adult females of the parasitoid lived longer when they had access to squash leaves than when only provided with water, and this increase in longevity was enough to allow maximum realized fecundity.

In even fewer cases, the abundance or effectiveness of parasitoids and predators were found not to be correlated with leaf trichome density (e.g., Sutterlin and van Lenteren 1997; Björkman and Ahrné 2005; see also reviews by Kennedy 2003; Simmons and Gurr 2005), possibly because of a reluctance to report 'negative' data.

The density of prey or hosts can affect the impact of leaf trichomes on predators and parasitoids, but relationships appear system-specific. In some studies, an effect of trichomes on natural enemies was detectable only at high prey/host densities (e.g., Sutterlin and van Lenteren 2000) while in other studies such an effect was observed only at low densities (Krips et al. 1999).

4.4.3 Adaptive Significance of Induced Trichome Production in Plants

The adaptive significance of damage-induced increases in trichome production should depend on the benefits and costs associated with this change in phenotype. Plants induced to increase leaf trichome density often receive less damage by insects than non-induced plants (Baur et al. 1991; Agrawal 1999; Dalin and Björkman 2003). This suggests that plants should benefit from induced trichome production as long as the fitness costs associated with increased trichome production do not exceed the benefits of reduced damage. Agrawal (1999) showed that induced wild radish plants (*Raphanus raphanistrum* and *Raphanus sativus*) received less damage by a variety of insects, and produced more seeds and fruits than non-induced plants. Wild radish responded to herbivory by producing new leaves with increased trichome density, but also with a systemic increase in the concentrations of secondary metabolites (Agrawal 1999). Thus, although this study clearly shows that the plants benefited from the induced responses, additional studies are needed to distinguish the effects of increased trichome production on fitness from those of other induced differences in plant quality in this and other species.

Apart from reducing overall damage, induced trichome production may divert damage away from the most valuable parts of the plant and cause insects to feed on other, less valuable leaves, or other non-induced plant individuals nearby. Because plants cannot change the density of trichomes on already existing leaves, an induced increase in trichome production can only be expressed in leaves developing during or subsequent to attack (Traw and Bergelson 2003). Induced increases in trichome production can however be relatively rapid and expressed in new leaves within days or weeks after the initial attack (Baur et al. 1991; Agrawal 1999; Dalin and Björkman 2003). A similarly rapid reduction in trichome production in new leaves

when damage ceases indicates that trichomes are costly to produce (Björkman et al. 2008). Additional evidence for costs of trichome production is provided by examples of trade-offs between trichome density and other putative defense traits, such as thorns (Björkman and Anderson 1990). A damage-induced increase in trichome production can lead to variation in trichome density within plants with older, basal leaves having lower trichome density than younger, induced apical leaves. Larvae of the leaf beetle *P. vulgatissima* showed a more dispersed feeding behavior among induced willow leaves with high trichome density at the top of shoots, indicating that the insects were searching for more optimal food within the branches (Dalin and Björkman 2003). Such damage-induced within-branch variation in trichome density may reflect developmental constraints, but may also be advantageous since damage to old basal leaves is likely to be less detrimental to plant fitness than damage to the young apical leaves (cf. Feeny 1976).

4.5 Perspectives

Several plant species respond to herbivory by producing leaves with increased density and number of trichomes. The apparent benefit of this response is to reduce further damage by making it more difficult for insects to feed on the leaves. However, the magnitude of induced trichome production may vary with habitat conditions, and increased trichome density may affect predators and parasitoids negatively, which could reduce the effect on leaf damage. Moreover, trichome production may also affect tolerance to drought and other forms of abiotic stress. Taken together, this suggests that an analysis of the adaptive significance of induced trichome production requires a multidimensional view of the realized fitness (see also chapter by Steppuhn and Baldwin this volume). The effects of induced trichome production on interactions with herbivores should not be examined in isolation, but has to be considered in the context of effects on tritrophic interactions, and the extent to which fitness costs and benefits vary with abiotic conditions in natural populations. More information is also needed on the genetic and hormonal basis of induced trichome production. Such knowledge could be important for the development of sustainable pest control methods, using induced plant responses as a tool to prevent insect pest damage in agricultural systems.

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